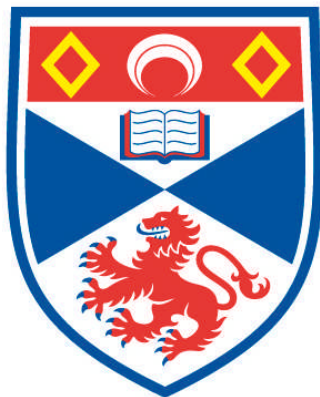


THE EFFECT OF WEIGHT ON HEALTH AND FACE PERCEPTION: A CROSS-CULTURAL PERSPECTIVE

Vinet Coetzee

**A Thesis Submitted for the Degree of PhD
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The effect of weight on health and face perception: a cross-cultural perspective

Vinet Coetzee

This thesis was submitted for the degree of Doctor of
Philosophy in August 2010

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Note to the reader

Throughout the experimental chapters in this thesis, I have used the pronoun 'we' instead of 'I'. This work is my own in terms of hypotheses, analyses and conclusions; however, the Perception Lab is an inherently collaborative environment with other members frequently assisting in the running of participants and the development of software. Such collaborative effort must be acknowledged. The plural pronoun reflects the fact that, if published, the following experiments would carry multiple authorship and is used in keeping with intellectual honesty.

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Abstract

My research identifies facial adiposity, a measure of weight in the face, as a novel facial cue to attractiveness and health. Previously identified facial cues, such as symmetry, averageness, sexual dimorphism and skin condition, are not consistently related to indices of actual health. In chapter 2 I demonstrate that facial adiposity is reliably associated with judgements of facial attractiveness and health in Caucasians and also with frequency and duration of respiratory infections, antibiotics use and blood pressure, indicating that facial adiposity is a valid cue to health. Additionally, in chapter 3 I identify three quantifiable facial shape cues that are reliably related to Body Mass Index (BMI) and are used by observers to judge weight in Caucasian and African faces.

In chapter 4 I show that Western Caucasian women, but not men, prefer a significantly lower facial adiposity when judging attractiveness than when judging health in other women's faces. This difference may reflect the influence of the media, since it was only significant in women's judgements and previous work showed that women internalize media messages about body ideals more than men do. In contrast, African participants in chapter 6 did not show any difference between the optimal facial adiposity for health and attractiveness, which is consistent with the prediction that people living in an environment with a high disease burden will base their concept of attractiveness more closely on cues to health. Importantly, these different patterns of results for Western Caucasian and African participants are unlikely to be due to cultural differences in media ideals of beauty, since the new African body ideal portrayed by the South African media is closely aligned with the Western ideal (chapter 5). Thus, my research suggests that perceptions of facial adiposity may well be influenced by an interaction between environmental factors and media ideals.

Chapter 1

The association between facial cues, attractiveness and health

To put the rest of the chapter in context, I will start with a brief review of the relevant topics in sexual selection theory.

1.1. Sexual selection

In his classic 1859 book, Darwin proposed the theory of sexual selection to explain the seemingly anomalous observation that certain secondary sexual ornaments appear to decrease the individual's ability to survive (Darwin, 1859, 1871). Male guppies, for example, have enlarged tails with colourful markings that makes them more conspicuous to predators (Gould & Gould, 1989). Sexual selection favours traits that enhance male-male combat ability and traits that enhance a male's attractiveness to females (Darwin, 1859, 1871). Females are expected to be the choosier sex because they invest more in their offspring than males (Trivers, 1972). Not only are eggs more costly to produce than sperm, but females incur additional costs through gestation and lactation (Clutton-Brock, Albon, & Guinness, 1989; Daly & Wilson, 1983; Trivers, 1972).

However, in monogamous species with biparental care, paternal investment can be quite costly and males are therefore also expected to be choosy (Trivers, 1972). Similarly, females are expected to compete with other females for access to resources, especially food resources (Daly & Wilson, 1983). Since choice is no longer only restricted to the females (female choice) and competition to males (male-male competition), these two types of selection can be more accurately described as intersexual selection (mate choice) and intrasexual selection (competition within a given sex; Barrett, Dunbar, & Lycett, 2002).

1.1.1. Mate choice

1.1.1.1. Direct and indirect benefits

Individuals choose their partners based on the direct and indirect benefits they can provide. Direct benefits have an immediate effect on reproductive success, and include non-genetic benefits such as, reduced risk of infection, increased resources and lower energy costs associated with finding conspicuous males (Halliday, 1983; Kirkpatrick & Ryan, 1991; Ryan, 1997). Indirect benefits refer to genetic benefits, which are passed onto the offspring allowing them to be of higher quality (Kirkpatrick & Ryan, 1991; Ryan, 1997).

There are various different hypotheses that explain mate choice through indirect benefits. In his theory of “runaway sexual selection” Fisher (1958) proposed that if a female with a preference for a trait mate with a male who has that trait, then their offspring will inherit both the trait and the preference. This can lead to a runaway process in which the traits become ever more exaggerated and individuals benefit from choosing the trait, not because of any direct benefits, but because their offspring will inherit the favoured trait (Fisher, 1958). This runaway process will only be stopped when it is countered by natural selection, that is to say when the exaggerated trait reduces the male’s survival ability too much (Fisher, 1958).

According to the “good genes” hypothesis, the other major point of view, genetic benefits are accrued through underlying genetic quality, or ‘good genes’, which are inherited by the offspring, improving their genetic quality (Andersson, 1994; Trivers, 1972; Zahavi, 1975). Zahavi’s (1975) handicap principle proposed that females assess male genetic quality by the size of the handicap they can survive with. Many sexually dimorphic traits increase male mortality (Ryan, 1997), therefore a male’s ability to survive with a handicap serves as an “honest signal” of his superior genetic quality. Low quality males simply cannot afford the handicap. Hamilton and Zuk (1982) proposed that these “good genes” could relate to resistance to parasites in the males. According to their hypothesis males bearing a comparatively low parasite load can fully express sexually selected traits such as bright plumage, which females can use as indicators of heritable parasite resistance (Hamilton & Zuk, 1982).

The immunocompetence handicap hypothesis builds on both the Zahavi (1975) handicap hypothesis and the Hamilton and Zuk (1982) parasite hypothesis, by positing an

interaction between the endocrine system and immune function. According to the immunocompetence handicap hypothesis, testosterone is responsible for the production of male secondary sexual traits, but is also an immunosuppressant (Folstad & Karter, 1992). Therefore males that display sexual traits fully, advertise that they are high-quality because they can contend with the immunosuppressive effects of testosterone (Folstad & Karter, 1992). There are, however, two underlying problems with the immunocompetence handicap hypothesis. First, although male-type behaviour and some secondary sexual traits are testosterone-dependent, other secondary sexual traits, such as male-type plumage are not always testosterone-driven, but are instead driven by the lack of oestrogen, increased luteinizing hormone or non-hormonal factors (Kimball & Ligon, 1999; Owens & Short, 1995). Second, a recent meta-analysis on the immunosuppressive effects of testosterone, concluded that testosterone appears to be immunosuppressive but only within certain taxa and for certain measures of immunocompetence (Roberts, Buchanan, & Evans, 2004).

To address the inconsistent relationship between testosterone and immunosuppression, Braude, Tang-Martinez and Taylor (1999) proposed the 'immune redistribution' hypothesis to explain findings that have been interpreted as an immunosuppressive effect of testosterone. According to the 'immune redistribution' hypothesis, testosterone temporarily shunts leucocytes (white blood cells) to areas of potential injury such as the skin, creating the impression that testosterone is immunosuppressive if immunity is accessed by leukocyte counts or if the measure of immunity is sampled at only one time or in only one tissue (Braude, et al., 1999).

1.1.1.2. Sex differences in mate preferences.

Human mate choice is a frequency dependent market, in which individuals with a high mate value are in demand and can choose among potential mates, while low mate value individuals struggle to obtain a mate (Buston & Emlen, 2003; Pawlowski & Dunbar, 1999). Health plays a crucial role in the mate value of both sexes (Symons, 1979; Thornhill & Gangestad, 1999a), but other factors such as age and resource acquisition also play a role in mate value (e.g. Symons, 1979; Trivers, 1972). Women only have a limited "fertile window" (Menken, Trussell, & Larsen, 1986; Symons, 1979), therefore men prefer younger women still in their fertile years (Buunk, Dijkstra, Kenrick, & Warntjes,

2001; De Sousa Campos, Otta, & de Oliveira Siqueira, 2002; Symons, 1995). This preference is especially pronounced in more traditional societies, where according to Pawlowski and Dunbar (1999) female market value peaks earlier.

Men, on the other hand, are fertile through most of their adult lives, thus according to Trivers (1972) a man's mate value is determined less by fertility and more by the external resources he can provide. Women are expected to choose men who indicate that they have the ability, and willingness, to invest resources in her and their offspring (Trivers, 1972).

Buss (1989) tested these predictions in 37 sample populations, drawn from 33 countries, by asking participants to rate the importance of 18 characteristics in choosing a partner, and the preferred age of a prospective partner. They found that women value cues to resource acquisition more highly than men, while men value physical attractiveness and relative youth more highly than women (Buss, 1989). These results have since been replicated for both sexes in other studies (Feingold, 1992; Pawlowski & Dunbar, 1999; Waynforth & Dunbar, 1995). In addition, Pawlowski and Dunbar (1999) found that age also plays a role in male mate value, not because of an association with fertility, but because of an association with the risk of future pair bond termination as a result of death or divorce.

1.2. Attractiveness related to mating success

Human mate choice studies generally assume that attractiveness is an important cue for mate choice, but relatively little empirical work has focused on the underlying assumption that attractiveness is closely related to mating success (Hönekopp, Rudolph, Beier, Liebert, & Müller, 2007; Kurzban & Weeden, 2005; Rhodes, Simmons, & Peters, 2005). Facial and bodily attractiveness is positively related to the number of self-reported sexual partners (Hönekopp, et al., 2007; Peters, Simmons, & Rhodes, 2008; Rhodes, et al., 2005), especially short term sexual partners in men (Rhodes, et al., 2005), and men's 'desirability' in dating encounters (defined as the frequency at which men are selected as a partner at speed dating events (Kurzban & Weeden, 2005). Men with attractive bodies also reported a younger age of first sex (Rhodes, et al., 2005). Perhaps the most convincing evidence for an association between male facial attractiveness and

reproductive success in a Western society comes from a large (N = 997 men) longitudinal study in Wisconsin, where the authors examined whether attractiveness assessed from yearbook photographs taken at age 18 years predicted the number of biological children at age 53 – 56 years (Jokela, 2009). They found that unattractive men on average produced 13% less children than moderately-to-very attractive men, partly because these unattractive men were less likely to get married (Jokela, 2009).

In women, facial and bodily attractiveness is positively related to 'desirability' in dating encounters (Kurzban & Weeden, 2005). In addition, facially attractive women report a higher number of long term sexual partners and a younger age of first sex than facially unattractive women (Rhodes, et al., 2005). Rhodes et al 2005 did not find a relationship between body attractiveness and any of the sexual behaviour measures in women, but since their participants were clothed and included a mix of different ethnicities little can be drawn from this finding at present. Ethnic variation in female fat distribution patterns could, for instance, have confounded perceptions of attractiveness. Pawlowski et al (2008) tested the association between facial attractiveness in early adulthood (18-27 years) and number of children at age 40+ in a group of 49 rural Polish women. The authors did not find an association between female facial attractiveness and number of children or grandchildren (Pawlowski, et al., 2008). However, in the large (N = 1244 women) longitudinal Wisconsin study, attractive and very attractive women (as assessed from facial photographs at age 18), had 16% and 6% more children at age 53-56 years than the combined group of not attractive and moderately attractive women, respectively (Jokela, 2009). This relationship between number of children and facial attractiveness was again partly mediated by the likelihood of getting married, in that attractive and very attractive women were more likely to get married than their less attractive counterparts (Jokela, 2009).

Taken together, these studies demonstrate that attractiveness does play an important role in mate choice decisions in both men and women. They also highlight some interesting context specific differences in the role of body and facial attractiveness. For instance, Rhodes et al (2005) concluded that attractive individuals are more successful at implementing their 'preferred' mating strategies (e.g. short term relationships in men and long term relationships in women). Short term relationships are expected to be more beneficial for men, because as opposed to long term relationships

their reproductive success is only constrained by the number of fertile women they can identify and inseminate in short term relationships. Women, on the other hand, require a long-term mate in order to secure paternal investment for her offspring (Buss & Schmitt, 1993). I will discuss the relative role of the face and the body in overall attractiveness in the next section.

1.3. Relative importance of face and body cues

Perceptions of facial and bodily attractiveness are closely correlated in women, irrespective of whether women are clothed (Peters, Rhodes, & Simmons, 2007; Rhodes, et al., 2005; Saxton, Burriss, Murray, Rowland, & Roberts, 2009) or nude (Thornhill & Grammer, 1999). Men's facial and bodily attractiveness are also positively correlated if men are photographed in the nude (Hönekopp, et al., 2007), with bare upper bodies (Fink, Täschner, Neave, Hugill, & Dane, 2010), or wearing shorts and a fitted undershirt (Peters, Simmons, et al., 2008) but not when they are wearing shorts and a T-shirt (Peters, et al., 2007; Rhodes, et al., 2005; Saxton, et al., 2009).

One interesting explanation for the discordance between male studies, but not female studies, is that muscularity might play a crucial role in male attractiveness (see discussion in section 1.7.3.1.3.2), while the Body Mass Index (BMI; weight scaled for height), or more specifically percentage body fat, might play a more important role in female attractiveness (see discussion in section 1.7.3.1.3.1). One might expect that our ability to estimate muscularity, compared to BMI for example, could be disproportionately affected by clothing. On the other hand, upper body strength, a measure of muscularity, can be accurately assessed from male faces (Sell, et al., 2009). It follows that male face and body attractiveness will be closely correlated when men's upper bodies are bare or covered with tight fitting clothing, but not when their upper bodies are covered in loose t-shirts. Furthermore, women's face and body attractiveness would be correlated irrespective of their clothing status. Thornhill and Grammer (1999) interpreted the high correlations between face and bodily attractiveness as an indication that the face and body represents a single ornament that signals quality. However, correlations between facial and bodily attractiveness are generally not very high ($r \sim 0.30$; Hönekopp, et al., 2007; Thornhill & Grammer, 1999), suggesting that not all aspects of facial and bodily attractiveness are linked.

One early study tested the relative roles of facial and body attractiveness in overall attractiveness by mixing and matching female faces and bathing suit clad bodies of varying attractiveness before having the resulting images rated for overall attractiveness (Alicke, Smith, & Klotz, 1986). Overall attractiveness ratings increased as face and body attractiveness ratings increased, but were lower if an attractive face was coupled with an unattractive body than *vice versa*, indicating that the body might be relatively more important than the face in overall attractiveness (Alicke, et al., 1986).

Other studies tested the relative contribution of the face and the body to overall attractiveness more directly, by having faces only, bodies only, and bodies with faces rated for attractiveness, before testing the relative predictive power of faces and bodies on overall attractiveness (Currie & Little, 2009; Mueser, Grau, Sussman, & Rosen, 1984; Peters, et al., 2007). Facial and bodily attractiveness were independently predictive of overall attractiveness in both sexes, but the face was a more powerful predictor than the body in women (Currie & Little, 2009; Mueser, et al., 1984; Peters, et al., 2007) and men (Currie & Little, 2009; Peters, et al., 2007), even when the bodies were presented semi-naked (Currie & Little, 2009).

Interestingly, Currie and Little (2009) found that although the face explained more of the variance in attractiveness judgments than the body in both short term and long term relationship contexts, the body was relatively more important in the short term than the long term relationship context. Confer, Perilloux, and Buss (2010) also found that when men are given the option to view either the face or the body when making a judgment on a woman's suitability for a short term relationship, they preferentially viewed the body. In contrast, men preferentially viewed the face when evaluating the woman for a long term relationship (Confer, et al., 2010).

Due to the widely reported correlation between facial and bodily attractiveness (Hönekopp, et al., 2007; Rhodes, et al., 2005; Thornhill & Grammer, 1999), multicollinearity could have been a problem in several of these studies (Currie & Little, 2009; Mueser, et al., 1984; Peters, et al., 2007), which would affect calculations regarding individual predictors of attractiveness (i.e. facial and bodily attractiveness; Garson, 2010a). Peters et al (2007) dealt with this problem in a separate analysis by first obtaining

attractiveness, symmetry, sexual dimorphism and averageness ratings for faces and bodies respectively. All these variables were entered into a principal components analysis (PCA), which produced two principal components, one representing the face and one representing the body, in both sexes. These uncorrelated principal components were used in a multiple regression analysis, with overall attractiveness as the dependent factor. In women, both facial and bodily attractiveness were predictive of overall attractiveness, but the face was a stronger predictor than the body (Peters, et al., 2007). Only facial attractiveness was predictive of overall attractiveness in men (Peters, et al., 2007). In section 1.7.3.1.3.2, I present evidence that muscularity might be the main predictor of male attractiveness. Since the men in this study were clothed, it is possible that women could access muscularity in the face but not the body, thereby increasing the relative predictive power of the face.

Taken together, these studies show that facial and body cues contribute independently to overall attractiveness in both sexes, but that facial cues seem to play a more important role in people's evaluation of overall attractiveness. Men do however shift their focus to the body somewhat when they are evaluating women for a short term relationship, although it is still unclear what the extent of this shift is. It is not clear why people pay more attention to facial cues when judging attractiveness, but there are various plausible explanations. First, the face could be more salient than the body because of its importance in social interactions, leading Barber (1995) to describe the face as an 'arena for sexual selection'. Second, because the face has a larger number of cues crammed into a smaller area, it allows the observer to quickly and accurately judge phenotypic quality. For instance, slight developmental imperfections, and therefore facial asymmetry, might become more obvious if the cues are located within closer proximity to one another. Lastly, perhaps the simplest explanation is that Western populations have 'learned' to rely less on body cues because these cues are frequently obscured by clothing in the current environment. People can quickly adapt their mate choice strategies to their environment (see discussion in section 1.7.4), thus Western people could have switched to preferentially using facial cues over body cues, although as we will see in section 1.7.3.1.3 the body is undoubtedly important in mate choice. It would be interesting to see whether populations that on average wear less clothing would rely more heavily on bodily cues.

1.4. Relationship between facial attractiveness and health

It is clear from the previous section that the face plays an important role in attractiveness. Since attractiveness is generally thought to serve as an important cue to reproductive value, which relies heavily on health (Symons, 1979; Thornhill & Gangestad, 1999a), it follows that attractive individuals are expected to be healthier. Yet, few empirical studies have tested the central claim that facial attractiveness is related to health. Judgements of facial attractiveness and perceived health are highly inter-correlated (Henderson & Anglin, 2003; Jones, Little, Feinberg, et al., 2004; Jones, et al., 2001; Kalick, Zebrowitz, Langlois, & Johnson, 1998; Law Smith, et al., 2006; Rhodes, Chan, Zebrowitz, & Simmons, 2003).

In contrast, facial attractiveness is not consistently linked to measures of actual health. The first study to test the facial attractiveness-actual health link found no significant correlation between late adolescent facial attractiveness and adolescent health scores, based on detailed medical histories between the ages of 11 and 18 (Kalick, et al., 1998). Late adolescent facial attractiveness was also unrelated to subsequent health scores based on a single medical examination by a medical doctor in mid adulthood (30-36 years) and late adulthood (58-66 years) in both sexes (Kalick, et al., 1998). A re-analysis of the data did find a significant relationship between late adolescent facial attractiveness and middle adult health scores in both sexes, but only when using faces below the median for attractiveness (Zebrowitz & Rhodes, 2004). However, adolescent health scores were unrelated to late adolescent facial attractiveness for faces above and below the median for attractiveness (Zebrowitz and Rhodes 2004). One major caveat of the Kalick et al (1998) data set, however, is the fact that the facial images were generally of very poor quality, in that they were black and white, not standardised for poser facial expression and had a very low resolution, since they were cropped from full body photographs taken in the late 1930's early 1940's. Thornhill and Gangestad (2006) did not find a significant association between facial attractiveness of standardised facial photographs and three health measures (the number and duration of respiratory and stomach infections and antibiotics use) for both sexes combined.

Inconsistent findings are also frequently observed between the sexes. Henderson and Anglin (2003) found that late adolescent facial attractiveness, assessed from

yearbook photographs in the 1920's, were positively related to longevity in men, while the relationship only tended to be significant in women. Similarly, Shackelford and Larsen (1999) showed that facial attractiveness significantly correlates with cardiovascular recovery time and self-reported frequency of sore throat/ cough in men, but not women. In women, facial attractiveness significantly correlated with self-reported frequency of headaches. Neither sex showed a significant association between facial attractiveness and five other self-reported symptoms, for example, runny or stuffy nose, jitteriness or trembling etc., but it must be said that the value of these self-reported symptoms are dubious. Hume and Montgomerie (2001) showed that attractive women report less severe diseases during their lifetime. No significant association was observed for the men.

Human Leucocyte Antigen (HLA) genes play a crucial role in the immune system and heterozygosity at these loci is thought to be associated with increased immune recognition of pathogens (Roberts, et al., 2005). One early study by Thornhill et al (2003) did not find any relationship between HLA heterozygosity and facial attractiveness judgments in male or female faces. Their study population was however very heterogeneous, including individuals of several different ethnicities and a large age range (men: 18-54 years; women: 17-44 years). It follows that the facial attractiveness judgments could have been confounded by age or own-ethnicity preferences. Later studies using more homogenous cohorts (young Caucasian adults) did find a positive association between male facial attractiveness and HLA heterozygosity (Lie, Rhodes, & Simmons, 2008; Lie, Simmons, & Rhodes, 2010; Roberts, et al., 2005). In contrast, HLA heterozygosity was unproductive of female facial attractiveness in a Caucasian (Lie, et al., 2008; Lie, et al., 2010) and African cohort (Coetzee, et al., 2007). Instead female facial attractiveness was positively associated with heterozygosity in genes unrelated to HLA genes (Lie, et al., 2008; Lie, et al., 2010).

Comparatively few studies have focused on the link between facial attractiveness and reproductive health. In non-makeup wearing women, facial attractiveness is positively associated with late follicular oestrogen levels (Law Smith, et al., 2006), which in turn is positively associated with conception in naturally cycling women (Lipson & Ellison, 1996). Two studies in men did not find a significant association between basal testosterone levels and male facial attractiveness (Penton-Voak & Chen, 2004), or male

overall attractiveness (face and body attractiveness combined; Peters, Simmons, et al., 2008). Soler et al (2003) found that male facial attractiveness is positively related to sperm morphology and mobility, but not concentration. However, a follow up study did not find a significant association between male overall attractiveness (face and body attractiveness combined) and sperm morphology, mobility or concentration (Peters, Rhodes, & Simmons, 2008). Since Peters et al (2008) did not report the specific association between facial attractiveness and sperm quality, it is difficult to say with certainty whether their results contradict those of Soler et al (2003) or not, although they did mention that separate face ratings of attractiveness, rather than the combined ratings of attractiveness made no qualitative or quantitative differences to the results.

Overall, the central relationship between facial attractiveness and actual health remains far from clear. In section 1.7, I will discuss various plausible reasons for the inconsistent relationship between facial attractiveness and actual health, but in order to understand the relationship between facial attractiveness and actual health more thoroughly, we first need to focus on the specific facial cues related to attractiveness, and their relationship with actual health. This will be the topic of my discussion in sections 1.5 and 1.6.

1.5. Facial cues related to attractiveness

Past research has identified four cues that determine facial attractiveness: symmetry, averageness, sexual dimorphism and colour/texture. These will be discussed in turn.

1.5.1. Symmetry

Over the past two decades research on facial symmetry has been prolific, driven mainly by the evolutionary viewpoint that symmetry indicates the ability to resist perturbations during development (Mather, 1953; Van Valen, 1962). Symmetrical individuals are therefore considered better quality mates and should in principal be considered more attractive (e.g. Grammer & Thornhill, 1994).

Another view, the perceptual bias view, attributes preferences for symmetry to the ease with which symmetrical stimuli can be processed in the visual system (Enquist & Arak, 1994; Johnstone, 1994). Two lines of evidence contradict a simple perceptual bias view. First, women prefer the scent of symmetrical men (Gangestad & Thornhill, 1998; Rikowski & Grammer, 1999; Thornhill & Gangestad, 1999b), and both sexes prefer the voices of symmetrical individuals (Hughes, Harrison, & Gallup, 2002), indicating that the preference for symmetry is not limited to the visual system. Second, Little and Jones (2003) demonstrated that symmetry preferences are greater when the face is in its natural upright (mate-choice relevant) position than when it is presented upside down (mate-choice irrelevant position). A simple inversion of the face would not have affected the ease with which the visual system could process the information, hence providing evidence against the simple perceptual bias view.

Studies testing the relationship between symmetry and attractiveness have produced inconsistent results depending on the method used to evaluate symmetry. Symmetrical faces are consistently judged more attractive when symmetry is estimated by rating unmanipulated faces for symmetry (Koehler, Simmons, Rhodes, & Peters, 2004; Rhodes, Proffitt, Grady, & Sumich, 1998; Rhodes, et al., 2005; Rhodes, Sumich, & Byatt, 1999; Rhodes, Zebrowitz, et al., 2001; Zebrowitz, Hall, Murphy, & Rhodes, 2002), or the 'perceptual' technique whereby left-left and right-right chimeras are constructed of the same face and then rated for similarity (Jones, Little, Feinberg, et al., 2004; Mealey, Bridgstock, & Townsend, 1999; Penton-Voak, et al., 2001). Similarly, studies that manipulate symmetry by transforming faces along a symmetry continuum normally find that symmetrical faces are judged more attractive (Koehler, Rhodes, & Simmons, 2002; Penton-Voak, et al., 2001; Perrett, et al., 1999; Rhodes, et al., 1998; Rhodes, Yoshikawa, et al., 2001; but see Swaddle & Cuthill, 1995). However, studies which produce symmetrical images by cutting the face along the facial midline and joining one side of the face and its mirror image together to form chimeras generally find a preference for asymmetry (Kowner, 1996; Noor & Evans, 2003). These equivocal findings can probably be attributed to the fact that chimeras typically display structural abnormalities around the facial midline (Perrett, et al., 1999; Rhodes, 2006), which might explain why people rate them less attractive.

More importantly, studies measuring symmetry directly often fail to correspond, with some studies finding a positive relationship between symmetry and attractiveness in both sexes (Grammer & Thornhill, 1994; Jones, et al., 2001), some studies finding a positive relationship only in female (Fink, Neave, Manning, & Grammer, 2006 only measured female faces; Hume & Montgomerie, 2001) or male faces (Penton-Voak, et al., 2001 only measured male faces; Rikowski & Grammer, 1999) and some studies not finding any significant relationship (Fink, Grammer, & Thornhill, 2001; Rhodes, Zebrowitz, et al., 2001; Roberts, et al., 2005; Shackelford & Larsen, 1997).

These inconsistent findings between studies measuring symmetry could partly be attributed to most studies' failure to isolate fluctuating asymmetry, which indicates developmental stability, from directional asymmetry, which does not (Mather, 1953; Palmer & Strobeck, 1992; Van Valen, 1962). Simmons et al (2004) measured both fluctuating and directional asymmetry and showed that directional asymmetry did not affect attractiveness judgements. Fluctuating asymmetry (and random deviations from directional asymmetry) contributed to the perception of attractiveness in male but not female faces (Simmons, et al., 2004). Koehler et al (2004) also isolated fluctuating asymmetry in a subset of the Simmons et al (2004) images, but found no association between fluctuating asymmetry and attractiveness in either sex, most likely because their smaller sample size reduced the power of the study to detect an association.

Studies measuring symmetry directly also often suffer from methodological constraints. For instance, slight lateral tilting of the face greatly influences symmetry measurements. Moreover, most studies use a limited set of 10-14 landmarks to define overall facial symmetry (Grammer & Thornhill, 1994; Hume & Montgomerie, 2001; Jones, et al., 2001; Penton-Voak, et al., 2001; Rhodes, Yoshikawa, et al., 2001; Rikowski & Grammer, 1999; Shackelford & Larsen, 1997). In a recent study, Komori, Kawamura, and Ishihara (2009) measured symmetry by: defining 72 facial landmarks and measuring the procrustes distance between each landmark and its corresponding mirror-reversed version. They found that symmetrical male, but not female faces, were considered more attractive (Komori, et al., 2009). Since Simmons et al (2004) and Komori et al (2009) are arguably the two strongest studies to test the symmetry-attractiveness link, it is interesting that both found an association between symmetry and attractiveness in male, but not female faces.

It is possible that other facial features might obscure indices of symmetry to varying degrees, causing measurement error. For example, fat deposits in the face could obscure skeletal features, adding more variability to symmetry measurements in individuals with a higher percentage body fat. As a consequence individuals with a higher percentage body fat might also seem less symmetrical, not necessarily because of developmental instability, but because of the measurement error induced by additional fat deposits. Since women generally have a higher percentage body fat than men (McArdle, Katch, & Katch, 2007; Meeuwsen, Horgan, & Elia, in press), this explanation would be consistent with the pattern of results observed by Simmons et al (2004) and Komori et al (2009). Indeed, Hume and Montgomerie (2001) found that BMI negatively predicts facial symmetry in women, but not men. Another interpretation for the symmetry-BMI link is, however, that individuals with a higher percentage body fat are generally in poor condition and therefore have a higher degree of developmental instability. Since percentage body fat contributes relatively more to female BMI than to male BMI (McArdle, Katch, & Katch, 2007; Meeuwsen, et al., in press), this interpretation would also be consistent with the symmetry-BMI link in women, but not men.

Overall, there is enough evidence to suggest that symmetry is attractive (particularly in men), although symmetry only accounts for ~25% of the variance in attractiveness (Rhodes, 2006), indicating a role for other facial cues in attractiveness.

1.5.2. Averageness

An average face has mathematically average trait values for a population. Symons (1979) hypothesised that average features could be functionally optimal as a result of the stabilising effect of natural selection. Individuals with average traits supposedly perform better at tasks such as chewing and breathing. Theoretically, averageness might also denote genetic heterozygosity, a predictor of a strong immune response (Thornhill & Gangestad, 1993).

Facial averageness is generally considered attractive, whether averageness is estimated by rating unmanipulated faces¹ (Rhodes, et al., 2005; Rhodes, Yoshikawa, et al., 2001; Rhodes, Zebrowitz, et al., 2001; Zebrowitz, et al., 2002), measuring the average procrustes distance between individual faces and the sex-specific average face (Komori, et al., 2009; Valenzano, Mennucci, Tartarelli, & Cellerino, 2006), or manipulated by transforming faces along an averageness continuum (Langlois & Roggman, 1990; Little & Hancock, 2002; Penton-Voak & Perrett, 2001; Rhodes, et al., 1999; Rhodes & Tremewan, 1996; Rhodes, Yoshikawa, et al., 2001). Rhodes et al (1999) only found a positive association between rated averageness and attractiveness in male faces (not in female faces), a finding that might be attributed to their small sample size (female N = 24), since a much larger study by the same authors found a positive association for both sexes (female N = 161; Rhodes, Zebrowitz, et al., 2001).

Although computer-averaged faces are more symmetric and have a more homogenous skin tone than individual faces, these attributes alone do not account for the attractiveness of average faces, as preferences for average shape remain when these factors are controlled for (Little & Hancock, 2002; Penton-Voak & Perrett, 2001; Rhodes, et al., 1999). Averageness is undoubtedly attractive, but it is not the only component that explains attractiveness. Perrett, May, and Yoshikawa (1994) and DeBruine et al (2007) showed that averageness is not optimally attractive. Both sexes prefer the face shape of an attractive composite (composed of a subset of attractive faces) to an average composite (composed of the full set of faces).

1.5.3. Sexual dimorphism

1.5.3.1. Femininity in female faces

Femininity is unmistakably attractive in women, presumably because it indicates a high oestrogen level (Law Smith, et al., 2006) and younger age within the population of sexually mature adults (Berry & McArthur, 1985; Perrett, et al., 1998), both crucial components of female reproductive function.

¹ Faces were actually rated for distinctiveness and the ratings reverse coded to produce an averageness measure.

Feminine female faces are rated more attractive, irrespective of the method used to assess or manipulate femininity (Cunningham, 1986; Fraccaro, 2010; Koehler, et al., 2004; Law Smith, et al., 2006; Little, Cohen, Jones, & Belsky, 2007; Penton-Voak, Jacobson, & Trivers, 2004; Perrett, et al., 1998; Rhodes, Hickford, & Jeffery, 2000; Rhodes, et al., 2005) and femininity accounts for ~64% of the variance in attractiveness judgements (Rhodes, 2006), indicating that facial femininity is a crucial component of female facial attractiveness.

1.5.3.2. Masculinity in male faces

A preference for masculinity is frequently explained in terms of the immunocompetence handicap hypothesis (Folstad & Karter, 1992; see discussion in section 1.1.1.1). Testosterone might not necessarily be immunosuppressive in all species; and does not seem to play a role in the development of all secondary sexual traits (see discussion in section 1.1.1.1). Testosterone is immunosuppressive in humans (Berczi, Lóránd, & Donna, 2005; Berczi, et al., 2003; Wyle & Kent, 1977), especially under conditions of trauma and shock (Berczi, et al., 2003), providing support for both the “immunosuppression” and “immune redistribution” hypotheses. However, the relationship between basal testosterone levels and male facial masculinity vary between studies, with one study finding a relationship (Penton-Voak & Chen, 2004), while most studies do not (Hönekopp, et al., 2007; Neave, Laing, Fink, & Manning, 2003; Peters, Simmons, et al., 2008). The facial masculinity-testosterone relationship might be qualified by testosterone response, rather than basal testosterone levels, as masculine men have a higher testosterone peak after ‘winning’ a competition than less masculine men (Pound, Penton-Voak, & Surridge, 2009).

Masculinity could also be preferred, simply because it provides the female with direct benefits. Due to their increased musculature and dominance (Mazur & Booth, 1998), masculine men are more likely to excel at intrasexual competition and provide much needed resources to the female. Indeed, facially masculine men have greater hand-grip strength, a measure of overall physical strength, than less masculine men (Fink, Neave, & Seydel, 2007). Women could therefore also prefer masculinity because it serves as a proxy for dominance and resource acquisition.

Nevertheless, women's preferences for male facial masculinity are variable (e.g. Grammer & Thornhill, 1994; Penton-Voak, et al., 2003; Perrett, et al., 1998). Studies which rate unmanipulated male faces for masculinity, or measure masculinity directly, find a general preference for masculinity in young adult male faces (Cunningham, Barbee, & Pike, 1990; Fink, et al., 2007; Grammer & Thornhill, 1994; Koehler, et al., 2004; Neave, et al., 2003; Penton-Voak, et al., 2001; Peters, Simmons, et al., 2008; Rhodes, et al., 2005; Scheib, Gangestad, & Thornhill, 1999), while Rhodes et al (2003) did not find a significant association between sexual dimorphism and attractiveness in adolescent male faces.

Studies that manipulate masculinity have variously observed a preference for femininity (DeBruine, Jones, Smith, & Little, 2010; Little, Burt, Penton-Voak, & Perrett, 2001; Little, Jones, Penton-Voak, Burt, & Perrett, 2002; Penton-Voak, et al., 2003; Penton-Voak, et al., 1999b; Perrett, et al., 1998; Rennels, Bronstad, & Langlois, 2008; Rhodes, et al., 2000; Welling, Jones, & DeBruine, 2008), a preference for masculinity (DeBruine, et al., 2006; DeBruine, Jones, Smith, et al., 2010; Feinberg, DeBruine, Jones, & Little, 2008; Johnston, Hagel, Franklin, Fink, & Grammer, 2001; Little, et al., 2007; Little, Jones, & DeBruine, 2008; Little, et al., 2010; Rennels, et al., 2008; Scott, Swami, Josephson, & Penton-Voak, 2008; Welling, et al., 2007b), or no preference for sexual dimorphism (DeBruine, Jones, Smith, et al., 2010; Penton-Voak, et al., 2003).

Some researchers have proposed that these inconsistent findings between masculinity manipulation studies can be attributed to the methods used to manipulate masculinity (Rennels, et al., 2008; Rhodes, 2006). Studies that manipulate masculinity by transforming male faces along a sexual dimorphism continuum (i.e. exaggerate differences between an average male and female face) generally find a preference for femininity (DeBruine, Jones, Smith, et al., 2010; Little, et al., 2001; Little & Hancock, 2002; Penton-Voak, et al., 2003; Penton-Voak, et al., 1999a; Perrett, et al., 1998; Rennels, et al., 2008; Rhodes, et al., 2000; Welling, et al., 2008), while studies that manipulate perceived masculinity (i.e. transform faces between a highly feminine and highly masculine male face) generally find a preference for masculinity (DeBruine, et al., 2006; DeBruine, Jones, Smith, et al., 2010; Little, et al., 2008; Little, et al., 2010; Rennels, et al., 2008). However, DeBruine et al (2006) and DeBruine et al (2010) compared masculinity preferences within-subject, using the sexual dimorphism and perceived masculinity manipulations, and found that masculinity preferences from both methods are

positively inter-related. Rennels et al (2008) did not find consistent masculinity preferences between the two methods using a between subjects design; finding a preference for femininity, and masculinity, using the sexual dimorphism and perceived masculinity manipulation, respectively. DeBruine et al (2010) replicated their study but found a general preference for femininity using both methods after controlling for non-face cues such as hairstyle. Taken together, these latter studies provide some evidence against a simple methodological explanation for the difference in masculinity preferences between studies.

An alternative explanation for the lack of consensus between masculinity manipulation studies is that people's preferences for masculinity are contingent on a variety of individual factors (e.g. Fink & Penton-Voak, 2002). Although masculinity is thought to signal male quality, both in terms of direct or indirect benefits (Folstad & Karter, 1992; Mazur & Booth, 1998), it is also associated with negative personality traits and behaviours. For example, masculine male faces are ascribed negative personality traits such as dishonesty, coldness, low emotionality, low cooperativeness and low quality as a parent (Boothroyd, Jones, Burt, & Perrett, 2007; Perrett, et al., 1998) and high-testosterone men are less likely to marry, more likely to divorce and more likely to be physically abusive than men with lower levels of testosterone (Booth & Dabbs, 1993; Mazur & Booth, 1998). Thus individual differences in masculinity preferences can be attributed to a trade off between the benefits (genetic quality) and costs (lower investment) associated with masculinity.

Relatively increased preference for masculinity are observed if women are more attractive (Little, et al., 2001; Penton-Voak, et al., 2003), in a relationship (Little, et al., 2008; Little, et al., 2002), healthier (Scott, et al., 2008), heterosexual (as apposed to homosexual; Glassenberg, Feinberg, Jones, Little, & DeBruine, 2009), have a higher conception risk (Johnston, et al., 2001; Little, et al., 2008; Penton-Voak, et al., 1999a; Welling, et al., 2007b), have higher testosterone levels (Welling, et al., 2007), have a higher sex drive (Welling, et al., 2008), have higher disgust sensitivity in the pathogen domain (DeBruine, Jones, Tybur, Lieberman, & Griskevicius, 2010) or had a good relationship with her parents (Boothroyd & Perrett, 2008). Women also show a relative increase in their preference for masculinity when they are judging attractiveness in a short term relationship context (Little, et al., 2007; Little, et al., 2002; Penton-Voak, et al.,

1999a; Scott, et al., 2008), judging attractiveness in a 'safe environment' context (Little, et al., 2007), if they live in an environment with a high disease burden (DeBruine, Jones, Crawford, Welling, & Little, 2010; Penton-Voak, et al., 2004) or if their reproductive strategy is to have fewer children (Moore, Smith, Cassidy, & Perrett, 2009). In sum, women seem most attracted to male facial masculinity when their own mate value is high and in contexts where we may suppose they are seeking a sexual partner that will provide them with 'good genes' for their offspring, but not necessarily substantial paternal investment.

Observer age is a potentially crucial explanatory factor for the discordance between masculinity manipulation studies, yet has received very little attention in the literature. Masculinity manipulation studies typically recruit observers within a large age range (17-50+ years). However, a recent study showed that observer age influences masculinity preferences, in that women within their reproductively active years prefer a significantly higher level of masculinity than young girls (< 15 years) or older woman (45+ years; Little, et al., 2010). The discordance between results of preferences in masculinity manipulation studies could therefore also be attributed to the large age ranges used in these studies.

In summary, sexual dimorphism preferences does seem to play a role in male facial attractiveness, but are contingent on individual observer factors that influence the trade-off between the benefits and costs associated with masculinity.

1.5.4. Skin condition

To date, very few empirical studies have focused on the relationship between skin condition and attractiveness. Apparent skin condition, as defined by the attractiveness (Jones, Little, Burt, & Perrett, 2004) and health (Roberts, et al., 2005) judgements of small patches of skin, influence male facial attractiveness independent of shape (Jones, Little, Burt, et al., 2004; Roberts, et al., 2005).

Skin homogeneity serves as an indicator of younger age and cumulative UV damage (Matts, Fink, Grammer, & Burquest, 2007), and might depict healthy levels of reproduction hormones (Fink, et al., 2001). Indeed, increased skin homogeneity is

considered more attractive in shape standardised female faces (Fink, et al., 2001). This preference for skin homogeneity has been replicated in a wider age range (Matts, et al., 2007) and in three-dimensional (3D) facial images (Fink, Grammer, & Matts, 2006).

Women are lighter skinned than men, and pale skin serves of an indicator of youth, parity and hormonal status, as skin darkens with age, during pregnancy and in the infertile phase of the menstrual cycle (for review see Symons, 1995; Van den Berghe & Frost, 1986). Pale skinned women are historically considered more attractive in a wide range of cultures (Van den Berghe & Frost, 1986), but recent work in modern Caucasian women's bodies found that, within the range tested, darker skin are considered more attractive (Smith, Cornelissen, & Tovée, 2007). Darker skinned Caucasian faces were also judged slightly more attractive, although the association was not significant (Fink, et al., 2001). Smith et al (2007) attributed this darker skin tone in Caucasians to increased skin tanning. When skin is exposed to sunlight, melanocytes increase their production of melanin, darkening the skin (Van den Berghe & Frost, 1986). In modern Western societies, skin tanning might serve as a status symbol, indicating that someone has sufficient time and resources for leisure activities, just as a paler complexion in the 18th century indicating that someone did not have to perform manual outdoor labour (Etcoff, 1999). A darker skin tone also partly denotes an increase in haemoglobin, the iron-containing pigment in red blood cells (Stamatas, Zmudzka, Kollias, & Beer, 2004).

A red skin tone may indicate higher blood circulation in peripheral vessels (Fink, et al., 2001), and has been linked to increased reproductive hormones in non-human primates (Czaja, Robinson, Eisele, Scheffler, & Goy, 1977; Rhodes, et al., 1997; Setchell & Dixon, 2001). Nevertheless, Fink et al (2001) did not find a significant association between skin redness [as measured on the Red Green Blue (RGB) spectrum] and attractiveness in unmanipulated, or shape standardised female faces. Bluer skin tone was, however, judged less attractive (Fink, et al., 2001). Interestingly, since yellow opposes blue on the RGB spectrum, an aversion to a blue skin tone could also be interpreted as a preference for a yellow skin tone.

In summary, increased skin homogeneity is consistently judged more attractive. Relatively darker skin might also be attractive in modern Caucasian populations, while there is little evidence to suggest that skin redness plays a role in attractiveness.

1.6. Relationship between facial cues and health.

In the previous section I showed that although there is some discordance between studies, there is sufficient evidence to suggest that, facial symmetry, averageness, sexual dimorphism and skin condition all serve as cues to attractiveness. Furthermore, the theory underlying the relationship between facial cues and attractiveness relies heavily on a proposed association with health. These cues should therefore also be considered healthy, and should be associated with actual health, but are they?

1.6.1. Symmetry

As a rule, symmetrical faces are judged healthier, irrespective of the method used to assess symmetry (Fink, Neave, et al., 2006; Grammer & Thornhill, 1994; Jones, et al., 2001; Penton-Voak, et al., 2001; Rhodes, et al., 2007; Rhodes, Zebrowitz, et al., 2001). Paradoxically, actual health is at best weakly associated with facial symmetry. Rhodes et al (2001) tested the association between symmetry (both measured and rated) of late adolescent faces and medically assessed childhood, adolescent, late adolescent and mid-adult health scores, in a large longitudinal study of 316 individuals born in the 1920's. They did not find a significant association between facial symmetry and any of the medically assessed lifetime health scores (Rhodes, Zebrowitz, et al., 2001). Similarly, Roberts et al (2005) did not find a significant association between measured symmetry and HLA heterozygosity in male faces.

Shackelford and Larsen (1997) measured facial symmetry and collected data on over 40 different self-reported health measures in two relatively small groups of young university students (~50 participants, both cases). They reported a significant association between facial symmetry and some of these self-reported measures, with more symmetrical people reporting better health (Shackelford & Larsen, 1997). However, some of their self-reported health measures were of questionable value, for example, participants were asked to report how often they had headaches, trouble concentrating, cried or had the urge to cry. Furthermore, they examined over a 1000 correlations across

the two studies, greatly increasing the probability of a type 1 error. Lastly, most of their significant findings did not replicate between the two studies.

Thornhill and Gangestad (2006) tested the association between measured symmetry in young adult faces and self-reported health measures (frequency of antibiotics use, number and duration of respiratory, and stomach or intestinal infections) in a large cohort of 406 university students. Men with more symmetrical faces reported a significantly lower number and duration of respiratory infections, but not stomach infections, or antibiotics use (Thornhill & Gangestad, 2006). There were no significant association between facial symmetry and any of the self-reported health measures in women (Thornhill & Gangestad, 2006). As proposed in section 1.5.1, facial fat deposits might obscure skeletal indices of symmetry, causing measurement error, particularly in women. The lack of a correlation between health measures and facial symmetry in women, but not men (Thornhill & Gangestad, 2006), could therefore be due to the confounding effect of facial fat on symmetry measurements.

Overall, although symmetrical faces are consistently judged more attractive, there is little evidence to support a link between symmetry and actual health, particularly in female faces. Rhodes and Simmons (2007) calculated the mean effect size of facial symmetry on health measures across studies. They concluded that the mean effect size was very small (0.04 ± 0.09) and not significantly different from zero (Rhodes & Simmons, 2007).

There are, however, several plausible explanations why these studies failed to find a link between facial symmetry and health. First, poor methodology might be to blame, as apart from the points mentioned above, none of the studies isolated fluctuating asymmetry which indicates developmental stability, from directional asymmetry which does not. All three studies also used a limited set of 10-14 facial landmarks to calculate overall facial symmetry. Second, as discussed earlier in this section, fat depots in the face might be obscuring skeletal features, making it difficult to measure symmetry accurately. Third, it is possible that modern medicine might have broken the link between symmetry and health. However, there was no association between symmetry and health in the Rhodes et al (2001) study cohort born in the 1920's before vaccinations and antibiotics were available. It would be interesting to see whether facial symmetry is

significantly associated with measures of health in a population with a high disease burden and poor access to medical care, for instance a rural African population.

1.6.2. Averageness

Average faces are generally perceived as healthier (Rhodes & Simmons, 2007; Rhodes, Zebrowitz, et al., 2001). Faces manipulated to appear more average are generally judged healthier in both sexes of Western, Asian, and Japanese faces (Rhodes, et al., 2007; Rhodes, Zebrowitz, et al., 2001), except in one group of Japanese men (Rhodes, et al., 2007). Studies testing the role of averageness on perceived health by rating unmanipulated faces for averageness and health are less consistent. In one study perceptually more average male, but not female, faces were judged healthier (Rhodes, et al., 2001), while in another perceptually more average female, but not male, faces were judged healthier (Rhodes, et al., 2007). The latter study was the stronger one of the two, however, since it had a much larger sample size ($N = 297$ compared to $N = 48$) and controlled for multiple correlations using Bonferroni corrections. Interestingly, although not significant (after Bonferroni correction) the effect size of male facial averageness on perceived health ($r = 0.26$) was fairly similar to the effect size observed in female faces ($r = 0.28$), indicating that rated averageness might also play a role in perceived health of male faces (Rhodes, et al., 2007).

Averageness is somewhat associated with actual health. The one study to test this relationship found that rated averageness of late adolescent faces were associated with medically assessed childhood health scores in men (but not women), late adolescent health scores in women (but not men), tended to correlate with adolescent health scores in women (but not men) and did not correlate with mid-adult health scores in either sex (Rhodes, Zebrowitz, et al., 2001). However, effect sizes were generally small to medium, explaining around 2-8% of the variance in actual health scores (Rhodes, Zebrowitz, et al., 2001). Overall, although average faces are generally perceived as healthier looking, the association between averageness and actual health is fairly inconsistent.

1.6.3. Sexual dimorphism

1.6.3.1. Femininity in female faces

Feminine female faces are judged healthier, irrespective of the method used to assess femininity (Law Smith, et al., 2006; Rhodes, et al., 2003; Rhodes, et al., 2007; Scott, et al., 2008).

However, femininity in female faces is not consistently linked to actual health. Rhodes et al (2003) did not find a significant association between rated femininity of late adolescent female faces and medically assessed adolescent health scores in a large cohort of 154 women, born in the 1920's. Measured femininity of young adult faces was weakly related ($r = 0.19$) to the number and duration of self-reported respiratory infections, but not stomach and intestinal infections, nor antibiotics use in women (Thornhill & Gangestad, 2006). In contrast, oestrogen levels were highly and positively related with perceptions of femininity ($r = 0.48$; Law Smith, et al., 2006), indicating a strong association between reproductive health and femininity. Overall, feminine female faces are considered healthier, but femininity is not consistently related to actual health.

1.6.3.2. Masculinity in male faces

Masculine male faces are judged healthier in some but not all studies. Two large studies of 130+ men found a positive relationship between rated masculinity and perceived health (Rhodes, et al., 2003; Rhodes, et al., 2007), while a third smaller study of 63 men did not (Penton-Voak, et al., 2007). Unfortunately Penton-Voak et al (2007) provided very little information about the male images used in the study, making it difficult to compare methodologies across studies. Several studies found no significant association between masculinity preferences and preferences for apparent health in faces manipulated along an apparent health and masculinity continuum (Boothroyd, et al., 2005; Boothroyd, et al., 2007; Boothroyd, Lawson, & Burt, 2009). On the other hand, Scott et al (2008) asked rural Malaysians to judge the apparent health of male faces manipulated along a sexual dimorphism continuum, finding that masculine faces were judged healthier.

Masculinity is fairly consistently related to actual health. Rhodes et al (2003) found a positive association between rated masculinity in young adolescent male faces and medically assessed adolescent health scores. Similarly, Thornhill and Gangestad (2006) showed that men with a higher level of measured facial masculinity report a lower

incidence of antibiotics use, a lower incidence and duration of respiratory diseases, but not a lower incidence of stomach and intestinal infections, than less masculine men. Overall, masculinity appears to be relatively consistently related to actual health but not perceived health.

1.6.4. Skin condition

Several studies show that skin condition plays an important role in health judgements. Fink et al (2006) applied the skin colour distributions of individual Caucasian women aged 11-76 years on shape standardised 3D faces. They found that the homogenous skin colour distribution of young women were rated healthier comparatively inhomogeneous skin colour distributions of more elderly women (Fink, Neave, et al., 2006). In a separate study, the relatively homogenous skin colour distribution of younger looking women was also judged healthier, even after Bonferroni corrections (Matts, et al., 2007). Matts et al (2007) then went further, by first analysing the overall skin homogeneity and then analysing the haemoglobin and melanin homogeneity in female skin patches. Overall skin homogeneity, haemoglobin homogeneity and to some extent melanin homogeneity were all positively associated with perceived health (Matts, et al., 2007).

Stephen, Law Smith, Stirrat, and Perrett (2009) tested the influence of skin redness on judgements of apparent health by asking Caucasian observers to manipulate skin colour along a red-green (CIELab a^*) axis, in order to optimise the healthy appearance of the face. Both male and female observers optimised healthy appearance by increasing redness above basal levels (Stephen, et al., 2009). Caucasian observers from the United Kingdom (UK) and African observers from South Africa (RSA) also increased skin redness in faces of various different ethnicities to optimise health (Stephen, Coetzee, Law Smith, & Perrett, 2009), indicating a cross-cultural preference for redness irrespective of the ethnicity of the face. In a third study, the authors manipulated Caucasian faces along two empirically-measured red pigment colour axis (i.e. oxygenated and deoxygenated blood axis; Stephen, et al., 2009). Once again, Caucasian observers increased skin blood colour, particularly oxygenated blood colour, above initial levels to optimise healthy appearance (Stephen, et al., 2009).

Stephen et al (2009) also tested the influence of skin yellowness and skin luminance on apparent health, using the same methodology, but instead manipulating faces along a blue-yellow (CIELab b^*) and separate dark-light (CIELab L^*) axis. Additionally, skin lightness and skin yellowness were manipulated simultaneously in a two dimensional skin colour transform. Observers increased skin yellowness and skin lightness in both single-axis and two dimensional trials (Stephen, et al., 2009). In human skin, CIELab b^* values are increased primarily by carotenoid (e.g. the yellow and red skin pigments obtained from fruit and vegetables) and melanin pigments, while CIELab L^* values are decreased by melanin but not carotenoid pigments (Stamatas, et al., 2004; Alaluf, et al., 2002). The preference for lighter, yellower skin therefore indicates a preference for carotenoid, but not melanin pigments, thus potentially indicating a preference for a healthier diet, but not skin tanning.

To my knowledge, there is only one study that tested the relationship between skin condition and actual health. Roberts et al (2005) tested the relationship between HLA heterozygosity and apparent health judgements of skin patches in male faces, and found that the two are positively related. HLA heterozygosity, thought to be associated with a more comprehensive immune response, were therefore associated with apparent skin condition, independent of facial shape information (Roberts, et al., 2005).

Overall, there is ample evidence to suggest that increased skin homogeneity is judged more attractive and healthy. Overall skin condition also seems to be related to actual health. Work on the relative importance of skin colour in health has only just taken off. So far there is a strong indication that relatively redder, yellower and paler skin increases the apparent health of skin, although their role in attractiveness is less clear. Interestingly, relatively darker skin seems to be considered more attractive in modern Caucasian populations, while relatively lighter skin seems to be considered healthier. Although future studies should investigate this discrepancy more directly before any definite conclusions can be made, it is possible that cultural factors (i.e. the status associated tanned skin) might have influenced attractiveness preferences, while leaving health preferences relatively untouched.

1.7. Reasons for poor relationship between facial attractiveness and health

It is evident from sections 1.4 to 1.6 that facial attractiveness, and its component cues, facial symmetry, averageness, femininity in female faces (but not masculinity in male faces) and skin condition are reliably perceived as healthier and more attractive. However, facial attractiveness and many of its constituent facial cues are only weakly associated with measures of actual health, aside perhaps from masculinity and skin condition which based on a limited number of studies seem to be related to some indices of actual health.

There are various plausible reasons why facial attractiveness and its component cues are not reliably linked to health. For one, health is a complex construct, consisting of various different components i.e. innate and adaptive immune response, reproductive and mental health etc.), which might not all be (a) measured accurately or (b) discernable from facial features. Additionally, It is often claimed that attractiveness preferences are invariant across different cultures (Cunningham, Roberts, Barbee, Druen, & Wu, 1995; Langlois, et al., 2000), yet what we consider attractive could be malleable by our environmental and cultural surroundings and even our own condition. Moreover, we might be overlooking an important facial cue, which might interact with other facial cues, obscuring the relationship between these cues and measures of health. Lastly, different facial cues could communicate different aspects of health, for example, femininity might be indicative of reproductive health but not of intestinal infections. In the next few sections, I will discuss the possible explanations for the discordance between facial attractiveness and health measures in more detail.

1.7.1. The way we measure health

According to the World Health Organization (WHO), health is defined as "a state of complete physical, mental, and social well-being and not merely the absence of disease or infirmity" (World Health Organization, 1946). Studies testing the association between facial attractiveness and health focus mostly on physical health, but have used a wide array of health measures, some of which can be measured more accurately than others. For example, some authors have criticized the use of self-reported health measures, indicating that these measures might be influenced by a person's affective state (Rhodes & Simmons, 2007). Unattractive individuals might have a more negative

affective state due to less favorable treatment by others, might report worse health, for instance more nausea, headaches etc., not because they more frequently experience these symptoms, but because they are more likely to recall negative experiences. The health measures used in these studies also tap into different aspects of health (i.e. cardiovascular efficiency, resistance to infectious diseases, reproductive health etc.) and differ in their ability to assess past, present and future health, which might not all be equally important when it comes to attractiveness. One way of guarding against these pitfalls associated with health measures, is to incorporate more than one health measure that measures different aspects of health and to include more direct health measures, such as blood pressure, instead of just relying on self-reported measures.

Moreover, since several different facial cues contribute to overall facial attractiveness, these cues could indicate different aspects of health, which might be more or less relevant depending on the context. For example, although a strong immune response might be crucial for male physical attractiveness, indicating an increased ability to provide resources and high quality offspring, reproductive health might be relative more important for female physical attractiveness, since men can maximize their reproductive effort by identifying women who are more likely to conceive. In support of this hypothesis, female attractiveness is strongly associated with reproductive health (Law Smith, et al., 2006), but not significantly associated with self-reported infections (Thornhill & Gangestad, 2006) or HLA heterozygosity (Coetzee, et al., 2007; Lie, et al., 2008; Lie, et al., 2010), two measures of the immune response. Studies could therefore benefit from focusing on health measures relevant to the facial cue in question.

Individuals that live in an environment with a high pathogen burden are expected to pay more attention to facial cues indicating a strong immune response than individuals that are exposed to a lower pathogen burden. For example, DeBruine et al (2010) showed that as the disease burden between countries increase, so to does the preference for masculinity in male faces, which is posited to serve as an indicator of a stronger immune system (Folstad & Karter, 1992). The role of environmental, conditional and cultural factors will be discussed further in section 1.7.4.

Kalick et al (1998) noted that apparent health could merely reflect an “attractiveness halo” whereby attractive individuals are judged more positively in general

(e.g. ascribed a higher IQ, pleasant personality etc.). It follows that apparent health might not be a very good health measure. As evidence for this, Kalick et al (1998) showed that the relationship between apparent health and adolescent health scores strengthen when attractiveness is controlled for, stating that “only with the distracting effects of attractiveness diminished did participants’ faces provide trustworthy cues to their health”. They interpreted this finding as an “attractiveness halo” for health judgements (Kalick, et al., 1998), but another interpretation is that apparent health provides an accurate estimate of health and that attractiveness depends not only on health but also on other factors.

If people can accurately assess health and not merely ascribe better health to more attractive individuals, one would expect actual health to be more closely correlated with apparent health than with attractiveness. There is some evidence for this, as Kalick et al (1998) themselves showed that apparent health judgements of late adolescent faces correlated with their concurrent medically assessed health scores in both sexes, while no such association existed for attractiveness. Law Smith et al (2006) also found a slightly stronger correlation between oestrogen levels and apparent health ($r = 0.52$), than between oestrogen levels and attractiveness ($r = 0.48$). The same pattern was observed for progesterone levels (apparent health: $r = 0.35$; attractiveness: $r = 0.33$; Law Smith, et al., 2006). However, Henderson and Anglin (2003) found that attractiveness, but not apparent health, was positively associated with longevity in both sexes. One could argue that longevity depends not only on the person’s inherent ability to ward off disease, but also depends on their access to medical care, nutritious food, etc. As a rule attractive individuals, particularly men, have a higher likelihood to succeed in the corporate world (Dipboye, Arvey, & Terpstra, 1976; Dipboye, Fromkin, & Wiback, 1975; Heilman & Saruwatari, 1979), thus are expected to be wealthier, have better access to medical care and consequently live longer. It is therefore unlikely that apparent health is merely a reflection of an “attractiveness halo”.

But how then do we explain that attractiveness and apparent health are highly inter-correlated (Henderson & Anglin, 2003; Jones, Little, Feinberg, et al., 2004; Jones, et al., 2001; Kalick, et al., 1998; Law Smith, et al., 2006; Rhodes, et al., 2003), while attractiveness is not consistently related to actual health (Coetzee, et al., 2007; Henderson & Anglin, 2003; Hume & Montgomerie, 2001; Kalick, et al., 1998; Law Smith,

et al., 2006; Roberts, et al., 2005; Shackelford & Larsen, 1999; Soler, et al., 2003; Thornhill & Gangestad, 2006; Thornhill, et al., 2003). One plausible explanation is that the limited set of health measures typically employed by studies testing the association between facial attractiveness cues and actual health, do not tap into the context-specific health measures, while apparent health does. It follows that both actual and perceived health measures are useful and should both be incorporated in future studies.

1.7.2. The way we measure facial cues

Studies testing the association between facial cues and health have assessed facial cues by perceptual methods, direct measurements and by manipulating facial cues. Just as with judgements of apparent health, judgements of facial cues, such as symmetry, sexual dimorphism etc., could also reflect an “attractiveness halo” (Jones, et al., 2001; Penton-Voak, et al., 2001). However, perceptual measures of facial symmetry, averageness and sexual dimorphism vary systematically with physical manipulations of these cues (Boothroyd, et al., 2005; Rhodes, et al., 2000; Rhodes, et al., 1998; Rhodes & Tremewan, 1996), indicating that people are judging these cues fairly accurately, but more work needs to be done before we can conclude that people are ‘face experts’ adept at estimating facial cues such as facial symmetry, masculinity etc. For one thing, different people could be interpreting concepts such as masculinity, distinctiveness and symmetry differently.

Direct measures of facial cues also have some drawbacks. Up to recently, direct measurements of symmetry and sexual dimorphism were fairly simplistic, relying on a limited number of facial landmarks (Cunningham, et al., 1990; Cunningham, et al., 1995; Grammer & Thornhill, 1994; Hume & Montgomerie, 2001; Jones, et al., 2001; Koehler, et al., 2004; Penton-Voak, et al., 2001; Rhodes, Zebrowitz, et al., 2001; Rikowski & Grammer, 1999; Scheib, et al., 1999; Shackelford & Larsen, 1997). As a general rule, direct measurements do, however, have the advantage of isolating the cue in question from other correlated cues, although this might not always be the case. For example, as mentioned earlier, facial fat could confound symmetry measurements, making heavier people appear more asymmetrical. Overall, each of the methods used to evaluate facial cues have their own pitfalls, and studies testing the relationship between facial cues and

health could incorporate more than one of these methods to provide a clearer picture of the association.

1.7.3. Are we missing facial cues to health and attractiveness?

Another possible explanation for the discordance between facial attractiveness cues and health, is that we might be missing an important facial cue to health and attractiveness. If multiple facial cues to health and attractiveness exist, and these cues vary independently, variance in an unacknowledged cue may disrupt the relationship between other facial cues and health. For instance, facial adiposity, or facial 'fat', a so far unacknowledged facial cue to health and attractiveness, could mediate or moderate the relationship between other facial cues (such as symmetry, sexual dimorphism, averageness and skin condition) health and attractiveness.

1.7.3.1. Facial adiposity as a cue to health and attractiveness?

There are several reasons to suspect that facial adiposity might be a valuable cue to health and attractiveness in the face. First, Hume and Montgomerie (2001) found that women, but not men, with a higher BMI are judged facially less attractive. An earlier study by Thornhill and Grammer (1999) did not find a significant association between BMI and female facial attractiveness, probably because they did not analyze the relationship appropriately. As we will see in section 1.7.3.1.3, BMI is curvilinearly related to attractiveness, a fact that Hume and Montgomerie (2001), but not Thornhill and Grammer (1999) took into account in their analysis. Second, previous studies have shown that BMI and more direct measures of adiposity, such as percentage body fat, are important cues to health and attractiveness in the body (see discussion in section 1.7.3.1.3). These measures of adiposity are not only related to perceptions of health, but they are also related to actual health. The World Health Organization classifies the BMI range as underweight ($\text{BMI} < 18.5 \text{ kg/m}^2$), normal weight ($18.5 - 25 \text{ kg/m}^2$), overweight ($25 - 30 \text{ kg/m}^2$) and obese ($\text{BMI} > 30 \text{ kg/m}^2$; World Health Organization, 2000), with the normal weight groups generally considered the healthiest. In section 1.7.3.1.2, I will discuss the health consequences of underweight, overweight and obesity in more detail.

If a cue is to serve as an indication of 'good genes' one implicit assumption is that the cue should be heritable. Studies involving adult twins, and adopted offspring, have demonstrated a high degree of heritability for BMI (~ 0.7), independent of the family environment (Allison, et al., 1996; Schousboe, et al., 2010; Sorensen, Price, Stunkard, & Schulsinger, 1989; Stunkard, Harris, Pederson, & McClearn, 1990; Stunkard, et al., 1986). Forbes, Sauer and Weitkamp (1995) showed a greater heritability in lean mass than fat mass in a group of 31 male and 56 female twin pairs. Forbes et al (1995) finding could be attributed to their relative over representation of female twins, as a recent study in a much larger group of 299 male and 325 female twins found that men show a greater heritability of percentage body fat (0.63) than lean mass (0.56), while women show the opposite (% fat: 0.59; lean mass: 0.61; Schousboe, et al., 2004 in Wells, 2010). Choosing a partner within the healthy weight range could therefore not only confer direct benefits, but also indirect benefits.

1.7.3.1.2. Fitness effects of fat

Adipose tissue plays an important role in reproductive fitness and sexual selection. Historically, fat reserves was seen as beneficial, protecting us from starvation and the cold, but the secular rise in obesity has also highlighted the negative consequences of excess fat reserves. In the next sections I will discuss the various fitness benefits and disadvantages of adipose tissue in more detail.

1.7.3.1.2.1. Buffering famine and short term energy fluctuations

During prolonged periods of negative energy balance, such as famines, fat reserves serve as an important determinant of survival (Norgan, 1997; Wells, 2006, 2010). It follows that obese individuals can accommodate famine for longer than lean individuals. Men and women vary in their ability to survive famines, with women surviving for longer periods (Menken & Campbell, 1992), presumably due to a difference in mean body fat content. Women have a higher percentage body fat than men (McArdle, Katch, & Katch, 2007; Meeuwsen, et al., in press). For instance, across a wide range of studies the average percentage body fat of young women and men was 25% and 14% respectively (McArdle, Katch, & Katch, 2007). However, women also have a higher percentage essential fat than men, calculated as 9% for women and 3% for men (Norgan, 1997).

Essential fat is defined as the fat stores needed for normal functioning, specifically the fat stores located in the bone marrow, heart, lungs, liver, kidneys, intestines, muscles and lipid-rich tissue of the central nervous system in both sexes. In women, the fat stores in the mammary glands, pelvic region and thighs are also classed as essential, although there is some debate as to whether they are strictly essential (Norgan, 1997). Taken together, the average woman can lose around 18% and the average man only around 12% of their body fat before they starve to death, accounting for the sex differences in survival. Studies have investigated the relative depletion of fat stores during starvation. Women with anorexia nervosa have a higher proportion of visceral compared to subcutaneous fat (Mayer, et al., 2005; Mayo-Smith, et al., 1989; Zamboni, et al., 2005), indicating a selective preservation of visceral fat during starvation.

In his seminal work, Neel (1962) proposed that “during the first 99 per cent or more of man's life on earth, while he existed as a hunter and gatherer, it was often feast or famine”. However, there is some debate as to whether famine has been a persistent selection pressure during our evolutionary past (Speakman, 2006; Wells, 2006, 2010). Recent evidence suggest that during the majority of our evolutionary history (the time spent as hunter-gatherers), famines were relatively infrequent and that it was only after the advent of agriculture, around 10, 000 years ago, that humans began to experience famines more frequently (Speakman, 2006; Wells, 2006, 2010).

In contrast, human populations frequently experience short term energy fluctuations due to seasonality, a common phenomenon in most parts of the world (Abdullah & Wheeler, 1985; Adams, 1995; Leonard & Thomas, 1989; Loutan & Lamotte, 1984). The tropics experience high seasonal variance in rainfall, whereas temperate latitudes are subject to seasonal variation in solar radiation, temperature and day length (Wells, 2010). These seasonal fluctuations are reflected in annual variation in weight, which typically range between 1 kg and 3 kg (Abdullah & Wheeler, 1985; Adams, 1995; Leonard & Thomas, 1989; Loutan & Lamotte, 1984), but can be as high as 5 kg (Wells, 2010). Adams (1995) showed that the seasonal weight loss in a group of adult agriculturalists in Mali was highly correlated with the reduction in percentage body fat, indicating that most of the weight loss was due to a loss in fat mass. In summary, fat reserves play a crucial role in buffering humans against periods of negative energy

balance, although it is more likely that fat stores evolved under conditions of short term energy fluctuations, rather than outright famines.

1.7.3.1.2.2. Adaptation to cold.

Adiposity is widely considered to be an adaptation to a cold environment and can contribute to thermoregulation in two ways (Wells, 2010). First, brown adipose tissue (BAT) can produce heat when the body is exposed to low environmental temperatures through the process of non-shivering thermogenesis (Cannon & Nedergaard, 2004). This thermoregulation ability is considered important in human infants as BAT is abundant during embryonic and early postnatal development (Cannon & Nedergaard, 2004). Brooke, Harris, and Salvosa (1973) compared the thermoregulatory capability of malnourished infants, which have low levels of BAT, before and after recovery. They showed that malnourished infants maintain a lower core temperature than recovered infants and that, upon exposure to cold temperatures (24-25 °C), malnourished infants' core temperature decrease continually, while recovered infants' core temperature stabilize towards the end of the cold stress (Brooke, et al., 1973).

Although brown adipose tissue is generally thought to be absent in human adults, recent studies using positron emission tomography, a nuclear imaging technique, indicates that adults retain BAT depots that can be induced in response to cold (Frühbeck, Becerril, Sáinz, Garrastachu, & García-Velloso, 2009; Nedergaard, Bengtsson, & Cannon, 2007). Brown adipose tissue might therefore also have a thermoregulatory function in human adults, especially those inhabiting colder climates, and warrants further research.

White adipose tissue could contribute to thermoregulation by (a) acting as an energy store for more general metabolic functions such as thermoregulation and (b) providing a layer of insulation (Norgan, 1997; Wells, 2010). Subcutaneous fat provides insulation against cold temperatures, especially during cold water submersion (Norgan, 1997). However, human populations that inhabit cold environments do not have a proportional increase in subcutaneous fat (Beall & Goldstein, 1992; Norgan, 1997; Risica, Ebbesson, Schraer, Nobmann, & Caballero, 2000; Wells, 2006, 2010). Risica et al (2000) showed that traditional Inuit communities in the Bering Strait, where the average winter

temperature is -26°C on the coast, have a high percentage body fat, ranging between 30-34% for women and 16-20% for men. Despite this high degree of body fat, Inuits have a high waist-to-hip ratio (WHR; ~ 0.94 for women; ~ 0.95 for men) and a high subscapular-to-tricep ratio (~ 1 for women; ~ 1.1 for men), indicating that most of the body fat is located in abdominal rather than subcutaneous deposits (Risica, et al., 2000). Similar research on pastoral nomads in Mongolia, where the average winter temperature is -20°C , found that the fat distribution of both sexes were predominantly abdominal. In women and children, the fat distribution were markedly more abdominal compared to other populations (Beall & Goldstein, 1992). It is therefore unlikely that insulation by means of subcutaneous fat plays an important role in cold adaptation. Instead, the predominantly abdominal fat distribution could be beneficial through other mechanisms, such as decreased surface-to-volume ratio of the body, reducing the surface area from which heat can escape (Beall & Goldstein, 1992). Since abdominal fat is positively associated with the basal metabolic rate (Olson, Heiss, Hirano, Brahler, & Beerman, 1998), a relative increase in abdominal fat can also increase heat production (Beall & Goldstein, 1992).

In summary, adipose tissue undoubtedly plays a role in the maintenance of body temperature in cold environments, although the exact mechanisms need to be clarified by future research.

1.7.3.1.2.3. Regulation of reproduction

Energy, and therefore fat reserves, is fundamental in reproduction. Women with low fat reserves, such as athletes and those with anorexia nervosa, frequently present with amenorrhea or anovulatory cycles (Crisp, Hsu, Harding, & Hartshorn, 1980; Golla, et al., 1981; Lake, Power, & Cole, 1997; Mitan, 2004; Ramos & Warren, 1995), which naturally hinders reproduction on the most basic level. Underweight women are also less likely to conceive (Zaadstra, et al., 1993). In their seminal work Frisch and co-workers proposed that there is a critical threshold of fatness necessary for the induction of menarche (Frisch, Revelle, & Cook, 1973) and ovulatory menstrual cycles (Frisch, 1990). Subsequent work found that ovarian function is more sensitive to energy balance (i.e. whether someone has a stable weight or losing/ gaining weight) and energy flux (i.e. absolute difference between energy intake and expenditure) than to fat stores, although all three are often correlated (Ellison, 2003).

It is not only the absolute amount of adipose tissue, but also the regional fat distribution of adipose tissue that is important in reproduction (Norgan, 1997). Men typically have an android fat distribution, with proportionally more fat stored in the abdominal region, whereas women tend to have a gynoid fat distribution, with proportionally more fat stored in the subcutaneous gluteo-femoral region (buttocks and thighs; Dixon, 1983; Norgan, 1997). These sex-specific fat distributions are caused primarily by sex hormones. Testosterone increases fat deposition in the abdominal region, whereas estrogen increases fat distribution in the gluteo-femoral region (Norgan, 1997; Rosenbaum & Leibel, 1999). The role of estrogen in the gynoid fat distribution is particularly evident at menopause, when women develop a more android fat distribution due to the cessation of estrogen (Rosenbaum & Leibel, 1999).

Gynoid fat distribution might be particularly important for reproduction, as lactation is primarily funded by the fat reserves in the buttocks and thighs. Rebuffe-Scrive et al (1985) showed that lipolysis, the breakdown of triglycerides into free fatty acids, was significantly higher in the femoral than the abdominal region during lactation. The femoral region fat depot is also particularly valuable to the offspring, since they contain a higher concentration of long-chain polyunsaturated fatty acids than the abdominal region (Phinney, et al., 1994). These polyunsaturated fatty acids are crucial for neural development in the offspring, as for example, polyunsaturated fatty acid supplementation in bottle-fed infants increase visual acuity (Markrides, Neumann, Simmer, Pater, & Gibson, 1995). Adipose tissue can also benefit female reproduction through the conversion of androgens to estrogens in adipose tissue, particularly the breast and abdominal fat depots (Nimrod & Ryan, 1975; Siiteri, 1987).

At the other end of the spectrum, obesity, particularly abdominal obesity, also inhibits reproduction. Obese women frequently present with menstrual cycle disorders, chronic or intermittent anovulation (Brown, Mishra, Kenardy, & Dobson, 2000; Hartz, Barboriak, Wong, Katayama, & Rimm, 1979; Lake, et al., 1997) and polycystic ovary syndrome (Gambineri, Pelusi, Vicennati, Pagotto, & Pasquali, 2002), all of which inhibit fertility. Obese women are also less likely to conceive (Zaadstra, et al., 1993) and more prone to maternal and fetal morbidity (Galtier-Dereure, Boegner, & Bringer, 2000). Compared to female studies, relatively few studies have looked at the association

between obesity and infertility in men. Those studies that have found that obese men have lower levels of circulating testosterone (Zumoff, et al., 1990) and are more prone to erectile dysfunction (Chung, Sohn, & Park, 1999; Shiri, et al., 2004) than normal weight men.

These negative effects of adiposity on reproduction are complex and still not completely understood (Azziz, 1989; Pasquali, 2006; Pasquali, Pelusi, Cenghini, Cacciari, & Gambineri, 2003). In women, obesity is associated with a relative sex hormone imbalance, leading to excess androgens (Pasquali, 2006; Pasquali, et al., 2003). In contrast to what has been observed in obese women, in the obese male total and free testosterone blood concentration levels progressively decrease with increasing body weight (Zumoff, et al., 1990), producing a condition of relative 'hypotestosteronemia' (Pasquali, 2006).

1.7.3.1.2.4. Immune function

Infection generates a significant energy demand, for instance an increased metabolic rate due to fever, the production and maintenance of lymphocytes, antibodies and other immune agents and the repair of damaged tissues (Ritz & Gardner, 2006; Scrimshaw & SanGiovanni, 1997; Wells, 2010). The availability of energy is therefore likely to play a critical role in the immune response to infection. Malnourished individuals, particularly those with protein-calorie malnutrition, are less immunocompetent (Marcos, Nova, & Montero, 2003; Neumann, et al., 1975; Ritz & Gardner, 2006) and more prone to infectious diseases (Ritz & Gardner, 2006; Shears, 1991). Despite this, studies testing the impact of anorexia nervosa on immunity find that although there is some immune impairment associated with anorexia, they are less frequent and less severe than would be expected given the extreme undernutrition associated with anorexia (Marcos, 2000; Marcos, et al., 2003). Women with anorexia nervosa frequently have mildly lower than normal white blood cell counts (leukopenia), a proportional increase in lymphocytes compared to other white blood cells (lymphocytosis) and a decreased delayed-type hypersensitivity skin response (Cason, Ainley, Wolstencroft, Norton, & Thompson, 1986; Marcos, Varela, Santacruz, Munoz-Velez, & Morande, 1993). However, Golla et al (1981) found that compared to controls, anorexia nervosa patients had normal lymphocyte counts and unimpaired mitogen-induced lymphocyte proliferation (an index of lymphocyte

function). Anecdotal evidence also suggests that women suffering from anorexia nervosa rarely develop the common cold or influenza (Armstrong-Esther, Lacey, Crisp, & Bryant, 1978; Golla, et al., 1981). Furthermore, Armstrong-Esther et al (1978) found a similar humoral antibody response against influenza and cell mediated immunity against tuberculosis between anorexic women and normal-weight controls. Women with anorexia nervosa typically consume a diet low in carbohydrates and fat, but fairly normal for other macro and micro nutrients (Marcos, et al., 2003). It follows that immune impairment might stem more from nutritional deficiencies, particularly protein deficiencies, rather than a lack of fat stores *per se*, except in extreme cases of undernutrition. One plausible explanation for the lack of significant immune impairment in individuals with 'undernutrition but not malnutrition' is that the immune system is prioritized over less crucial functions, such as the reproductive function, when resources are scarce.

Nevertheless, adipocytes are intricately associated with the immune system. Wells (2010) proposed four ways in which adipose tissue can benefit the immune response directly. First, as mentioned previously, adipose tissue can provide the energy required for immune function. Second, adipose tissue, especially visceral depots, secretes pro-inflammatory cytokines which promote the immune response by causing inflammation. Third, adipose tissue also secretes a range of anti-inflammatory cytokines and growth factors that could aid in the repair of damaged tissues. Lastly, recent work indicates that leptin (a hormone produced by adipose tissue and involved in the regulation of appetite) plays a regulatory role in the immune response (Fernández-Riejos, et al., 2010; Lam & Lu, 2007).

At the other end of the spectrum, several studies show that obese individuals have a higher susceptibility to infection than their non-obese counterparts. In a large study of 78062 women aged 27 to 44 years, obese women had a 2.2 fold increased risk of developing community-acquired pneumonia compared to normal weight women, with similar associations seen after excluding past and current smokers (Baik, et al., 2000). Compared to normal weight men, obese men had a slightly increased risk (relative risk 1.1) of developing community-acquired pneumonia in a sample of 13604 men aged 44-60 years (Baik, et al., 2000). Similarly, overweight children (defined as a BMI ≥ 20 ; 90th percentile) are more likely to develop acute respiratory infections, and chronic respiratory symptoms, than low or normal weight children (Jedrychowski, Maugeri, Flak, Mroz, &

Bianchi, 1998). Lastly, obese surgical patients are more likely to develop post-surgical infections than non-obese surgical patients (Choban, Heckler, Burge, & Flancbaum, 1995; Vilar-Compte, et al., 2000).

The mechanisms that predispose obese individuals to infections are poorly understood in humans (Falagas & Kompoti, 2006; Marcos, et al., 2003; Marti, Marcos, & Martinez, 2001). Obesity is associated with a state of low grade systemic inflammation, as measured by C-reactive protein levels, in adults (Visser, Bouter, McQuillan, Wener, & Harris, 1999) and children (Visser, Bouter, McQuillan, Wener, & Harris, 2001). Increased BMI is also associated with leucocytosis, or increased white blood cell counts (Nieman, et al., 1999; Tanaka, et al., 1993; Visser, et al., 2001), confirming the presence of low-grade systemic inflammation. Since leucocytosis is commonly accompanied by a relative increase in immature compared to mature leucocytes (Abramson & Melton, 2000), the efficacy of lymphocytes could be affected. Indeed, both studies also reported a reduction in lymphocyte responsiveness to mitogens in obese compared to non-obese individuals, indicating an impairment of the immune response (Nieman, et al., 1999; Tanaka, et al., 1993). This low grade systemic inflammation associated with obesity might be due to the secretion of pro-inflammatory cytokines by adipose tissue (Dandona, Aljada, & Bandyopadhyay, 2004; Visser, et al., 2001). Another plausible explanation for the link between obesity and chronic inflammation is that obese individuals have a higher intake of glucose and macronutrients, which even at normal intake levels cause a transient increase in oxidative stress and inflammatory response (Dandona, et al., 2004).

1.7.3.1.2.5. Other health consequences of fat

The secular rise in obesity has highlighted the disadvantages of excess fat. In his review of the medical hazards of obesity, Pi-Sunyer (1993) concluded that obesity is associated with a range of conditions, namely increased hypertension, dyslipidemia, coronary heart disease, type 2 diabetes, gallbladder disease, respiratory disease, gout, arthritis and some forms of cancer. For the purpose of this discussion I will focus mainly on the obesity related increased risk of cardiovascular disease (which includes coronary heart disease and stroke) and type 2 diabetes.

According to the International Diabetes Federation abdominal obesity is a fundamental part of a cluster of conditions, collectively known as the metabolic syndrome (Alberti, Zimmet, & Shaw, 2005). These conditions also include raised blood pressure, raised glucose levels, raised triglyceride levels and reduced HDL-cholesterol, and are strongly associated with the development of type 2 diabetes and cardiovascular disease (Alberti, et al., 2005).

Various studies have linked excess fat, particularly abdominal fat, with an increased risk of developing cardiovascular disease, type 2 diabetes and overall mortality (Balkau, et al., 2007; Despres & Lemieux, 2006; Manson, et al., 1995; Willett, Dietz, & Colditz, 1999; Willett, et al., 1995). For example, a large follow-up study of 115 818 female Nurses examined the association between BMI and the incidence of coronary heart disease (CHD; Willett, et al., 1995). Controlling for age, smoking, menopausal status, postmenopausal hormone use and parental history of CHD, the relative risk for CHD increased with a rise in BMI (Willett, et al., 1995). Compared to women with a BMI of less than 21 kg/m², heavier women below a BMI of 23 kg/m² had a relative risk of 1.2, followed by a relative risk of 1.5 (23-25 kg/m²), 2.1 (25-29 kg/m²) and 3.6 (> 29 kg/m²; Willett, et al., 1995). Willett et al (1999) extended these findings to type 2 diabetes and men by demonstrating that a BMI increase above 21 kg/m² produced a sharp increase in the relative risk of type 2 diabetes and a more moderate but substantial increase in the relative risk of hypertension and coronary heart disease for both sexes (Willett, et al., 1999). Using the Nurses health study data, Manson et al (1995) showed that increased BMI was also strongly associated with increased mortality of all causes. Compared to the reference population of < 19 kg/m², heavier women had an increased relative risk of overall mortality, culminating in a relative risk of 2.1 for women with a BMI larger than 29 kg/m² (Manson, et al., 1995). Balkau et al (2007) tested the relative influence of BMI and waist-circumference (a measure of abdominal obesity) on cardiovascular disease and type 2 diabetes in a large study of 68 409 men and 98 750 women in 63 countries. They found that both waist-circumference and BMI were independently associated with cardiovascular disease and type 2 diabetes in both sexes (Balkau, et al., 2007). However, the age-and-region adjusted odds ratios were higher for waist circumference than for BMI in both sexes and for both cardiovascular disease and type 2 diabetes (Balkau, et al., 2007), indicating that abdominal obesity was a more important determinant of these risk factors than obesity *per se*.

1.7.2.1.2.6. Summary

It is clear from the previous sections that a certain degree of adipose tissue is beneficial in that it buffers the individual against low (or fluctuating) resources, protects against cold temperatures, is fundamental for reproduction and plays a role in the immune function. Ironically, however, adipose tissue suppresses reproductive and immune function when it is present in excess amounts, while also predisposing the individual to a range of metabolic and non-metabolic diseases. Thus there is a substantial body of evidence linking the relative amount and distribution of adipose tissue to health and survival.

1.7.3.1.3. The role of BMI and WHR in the perception of bodily attractiveness and health

In the previous section we saw that the relative amount and distribution of adipose tissue is related to health in both sexes. But if measures of overall body weight, such as BMI and percentage body fat, and measures of body fat distribution, such as WHR are to play a role in mate choice, these measures must also be associated with attractiveness judgements. In the next two sections I will review the available evidence linking various measures of overall body weight and regional fat distribution with apparent bodily attractiveness and health.

1.7.3.1.3.1. Female bodies

Overall body weight and the regional distribution of adipose tissue have both been shown to contribute to the perception of attractiveness in men and women (for review see Bateson, Cornelissen, & Tovée, 2007; Swami, 2006; Symons, 1995; Weeden & Sabini, 2005). As discussed in section 1.7.3.1.2, both the relative amount and the regional distribution of body fat play an important role in health and reproduction. Early work focused primarily on the role of WHR on female attractiveness. Singh (1993) assessed the role of WHR on attractiveness using simple line drawings of Caucasian female bodies that varied in four levels of WHR (0.7 - 1.0) and three levels of body weight (underweight; normal weight; overweight; Singh, 1993). Western male observers judged a WHR of 0.7

most attractive (Singh, 1993), a results that was replicated for Western observers of both sexes using the same Caucasian stimuli set (Furnham, Tan, & McManus, 1997; Marlowe & Wetsman, 2001; Singh, 1994; Tassinari & Hansen, 1998; Wetsman & Marlowe, 1999). The only exception was a study by Henss (1995) which found no significant attractiveness difference between a WHR of 0.7, 0.8 and 0.9. Henss (1995), however, used a between subject design (the other studies used a within subject design) which would have reduced the statistical power to detect differences in their study.

Studies using the Singh (1993) stimuli set consistently found that Western observers judge overweight drawings less attractive than under-or-normal weight drawings (Furnham, et al., 1997; Henss, 1995; Singh, 1993, 1994; Tassinari & Hansen, 1998; Wetsman & Marlowe, 1999). Underweight female drawings were generally judged less attractive (Furnham, et al., 1997; Singh, 1993, 1994; Wetsman & Marlowe, 1999), although Tassinari and Hansen (1998) and Henss (1995) found that underweight figures were judged similar or more attractive than normal weight figures.

Cross-cultural studies indicate that a normal weight figure with a WHR of 0.7 is by no means universally attractive. Yu and Shepard (1998) tested the attractiveness preferences of three groups of Matsigenka indigenous men from Southeast Peru. Matsigenka men from the most isolated parts judged overweight line drawings with a WHR of 0.9 most attractive, ranking images first by weight and then by WHR (Yu & Shepard, 1998). Mildly acculturated Matsigenka men also preferred overweight figures, while the most acculturated Matsigenka men showed similar preferences to that of Western Caucasian men, judging a normal weight, WHR 0.7 figure most attractive (Yu & Shepard, 1998). Similarly, hunter-gatherer Hadza men of Tanzania base their attractiveness preferences primarily on weight and not WHR and also judged the overweight line drawings with a WHR of 0.9 most attractive (Wetsman & Marlowe, 1999). When Marlowe and Wetsman (2001) presented the Hadza men with another set of line drawings varying only in WHR (0.4-1.0), Hadza men still preferred a high WHR of 0.9. Indigenous Shiwiar men of Ecuadorian Amazonia also found the overweight female figure most attractive, basing their attractiveness preferences on weight and not WHR (Sugiyama, 2004).

Although the use of line drawings made a substantial contribution to our understanding of the role of overall body weight and WHR in female attractiveness, they suffered from several drawbacks. First, Tassinari and Hansen (1998) noted that the Singh (1993) image set confounded weight with hip size, as well as WHR with relative waist size and did not systematically examine WHRs of less than 0.7. To account for these concerns Tassinari and Hansen (1998) developed a new female Caucasian stimulus set that varied in weight (light, moderate and heavy), waist size (small, medium and large) and hip size (small, medium and large), expanding the WHR range to include lower WHR values (0.5-0.9). They found that, hip size more strongly predicted attractiveness than WHR. Moreover, they found that body weight more strongly predicted attractiveness than WHR (Tassinari & Hansen, 1998), highlighting the importance of body weight in attractiveness judgments.

Second, some of the manipulations may result in images outside the natural range of variation in the population, and as a result lack ecological validity (Bateson, et al., 2007). The problem of ecological validity is further compounded in the cross-cultural work, since the line drawings depicted Caucasian women and were developed based on a Western Caucasian population. The use of such stimuli produces two main problems. First, population means for overall weight and WHR's might differ between the Western Caucasian population and the tested population. For instance, Sugiyama (2004) noted that the 'high' WHR line drawings were actually average WHR for Shiwiar women, thus the Caucasian image set did not include images that were 'high' WHR by Shiwiar standards. Second, there is a more general problem with using Caucasian stimuli for studies involving other ethnicities. Other ethnicities might not judge Caucasian stimuli in the same way that they would judge stimuli of their own ethnicity. For instance, both Japanese and British men preferred a greater degree of feminization for faces from their own population than for faces from the other population (Perrett, et al., 1998), a result that was later also replicated for Jamaican and British men (Penton-Voak, et al., 2004). Thus it is probably unwise to extrapolate cross-cultural findings beyond the given test situation. We can only really infer what these ethnicities find attractive in Caucasian women, not what they find attractive in their own ethnicity.

Another problem with the use of modified line drawings is that when the figures are modified by altering the width around the waist, this not only alters the WHR, but also

the apparent BMI. Consequently, as the WHR increases so to does the apparent BMI, making it difficult to determine whether changes in attractiveness ratings are made on the basis of WHR, BMI, or both (Symons, 1995; Tovée & Cornelissen, 1999; Tovée, Maisey, Emery, & Cornelissen, 1999). The use of unmodified photographic images circumvents this problem, making it possible to determine the relative contribution of WHR and BMI to attractiveness.

In a study using unmodified body images, Tovée, Reinhardt, Emery, and Cornelissen (1998) quantified the relative importance of BMI compared to WHR in predicting female physical attractiveness. They showed that BMI explained 74% of the variance in female attractiveness compared to only 2% by WHR (Tovée, et al., 1998). This finding has been replicated in a wide range of observer populations, in which BMI explained between 58 and 86%, while WHR only explained between 0 and 30% of the variance in female attractiveness in 2D front-view (Swami, Antonakopoulos, Tovée, & Furnham, 2006; Swami, Caprario, Tovée, & Furnham, 2006; Swami, Knight, Tovée, Davies, & Furnham, 2007; Swami, Miller, Furnham, Penke, & Tovée, 2008; Swami, Neto, Tovée, & Furnham, 2007; Swami & Tovée, 2005a; Swami & Tovée, 2007a; Swami & Tovée, 2007; Swami & Tovée, 2007b; Tovée & Cornelissen, 2001; Tovée, et al., 1999; Tovée, Swami, Furnham, & Mangalparsad, 2006) and 2D profile images (Tovée & Cornelissen, 2001). Similarly, in 3D female bodies, BMI accounted for 73% of the variance in perceived attractiveness, while WHR only accounted for 1% of the variance (Fan, Liu, Wu, & Dai, 2004).

It is however possible that the relative importance of BMI might have been inflated if the BMI range was consistently larger than the WHR range. Tovée, Hancock, Mahmoodi, Singleton, and Cornelissen (2002) addressed this problem by selecting a subset of female images within a limited BMI range (18–26 kg/m²), while placing no restrictions on the WHR range. In addition to restricting the BMI range, they also disrupted the naturally positive relationship between BMI and WHR in a second experiment by selecting images in which BMI and WHR were reverse-correlated (i.e. high BMI-low WHR and *vice versa*; Tovée, et al., 2002). Observers rated both sets of images for attractiveness. Their results show that even with these restrictions on the BMI range, BMI was still a stronger predictor of female attractiveness than WHR (Tovée, et al., 2002). Additionally, in the second experiment, low BMI-high WHR images were rated

more attractive (Tovée, et al., 2002), indicating that if observers had to choose between an 'attractive BMI' and an 'attractive WHR', they chose the 'attractive BMI'. Cornelissen, Hancock, Kiviniemi, George, and Tovée (2009) provided further evidence for the relative importance of BMI over WHR. They recorded the eye movements of three groups of male and female observers asked to judge female images for attractiveness, body fat and WHR, respectively (Cornelissen, Hancock, et al., 2009). When asked to judge attractiveness, observers' eye movements clustered in the central and upper abdomen, the same area they focused on to judge body fat, but not the same area they focused on to judge WHR (Cornelissen, Hancock, et al., 2009). Although the debate about the relative importance of WHR still rages on (Cornelissen, Toveé, & Bateson, 2009; Dixon, Li, & Dixon, 2010; Dixon, Sagata, Linklater, & Dixon, 2010; Singh, 2002, 2006; Singh, Dixon, Jessop, Morgan, & Dixon, 2010; Tovée, Furnham, & Swami, 2007) it falls slightly outside the scope of this thesis. I think there is sufficient evidence to conclude that even though WHR and BMI are both significant predictors of female attractiveness, BMI is a more important predictor than WHR.

Interestingly, in a recent study Rilling, Kaufman, Smith, Patel, and Worthman (2009) found that although BMI was more strongly correlated with female attractiveness (front-view) than WHR, abdominal depth (an anterior-to-posterior measurement taken in the sagittal plane that reflects the depth of the lower torso at the umbilicus) and waist-circumference were more strongly correlated with female attractiveness than both BMI and WHR. However, these authors assumed a linear relationship between all the anthropometrical measures and attractiveness, which might be true for abdominal depth and waist circumference, but is not true for either BMI or WHR. The predictive power of BMI and WHR would therefore have been underestimated. It would be interesting to see if abdominal depth and waist-circumference would still predict female attractiveness more strongly than BMI and WHR if the data is analyzed appropriately.

But is there an optimum BMI considered most attractive? Tovée et al (1998) found a curvilinear relationship between BMI and attractiveness judgments of unaltered female Caucasian images. British men judged women with an intermediate BMI more attractive than both high-and-low BMI women, with the polynomial regression curve reaching a peak for attractiveness at around 20 kg/m² (Tovée, et al., 1998). A wide range of follow up studies confirmed that British men and women of various different ethnicities judged

Caucasian female images with a BMI ranging between 19 and 21 kg/m² most attractive (Swami, Antonakopoulos, et al., 2006; Swami, Neto, et al., 2007; Swami & Tovée, 2005a; Swami & Tovée, 2007; Tovée, Emery, & Cohen-Tovée, 2000; Tovée, et al., 2006). Men from urban populations in four other European countries, namely Greece (Swami, Antonakopoulos, et al., 2006), Spain, Portugal (Swami, Neto, et al., 2007) and Finland (Swami & Tovée, 2007), also found a narrow range of 20 to 21 kg/m² most attractive when judging the same set of Caucasian female images. Even urban men from non-European countries as far a field as Thailand (Swami & Tovée, 2007a), Malaysia (Swami & Tovée, 2005a) and adolescent boys from Samoa (Swami, Knight, et al., 2007) agree that a female BMI within this narrow range (19-21 kg/m²) is most attractive. The only urban group that preferred a BMI slightly below this narrow range (19-21 kg/m²) were Japanese men, who found a BMI of 18 kg/m² most attractive (Swami, et al., 2006). One intriguing explanation for the low BMI preference of Japanese men is that the media might disproportionately affect Japanese men's preferences due to the strong emphasis on conformity to social norms in Japanese culture (Swami, et al., 2006). I will discuss the mediating effect of the western media, and other sociocultural pressures, in detail in chapter 4. Asian populations do however have an increased risk for developing type 2 diabetes and cardiovascular disease at a comparative lower BMI than Western populations (World Health Organization expert consultation, 2004), thus Japanese men's preferences for a relatively lower BMI might also reflect a cultural difference in the association between BMI and health. Taken together, these studies strongly suggest that people from urban populations all over the world find women within a very narrow BMI range most attractive, irrespective of their ethnicity and nationality. A recent study tested the association between female attractiveness and a percentage body fat, a more direct measure of body fat mass than BMI. The authors videotaped a 360° view of rotating semi-clad Caucasian women and found that within the normal BMI range, women with a higher percentage body fat were rated less attractive (Smith, et al., 2007). Although percentage body fat is expected to be more closely related to female attractiveness than BMI, it would be interesting to see if this really is the case, and further, what percentage of the variance in attractiveness each of the measures explain.

Rural populations show very different weight preferences. Swami and Tovée (2005a) compared the female attractiveness preferences of three groups of ethnic Malaysian males and females, the first group was from Kuala Lumpur, the largest city in

Malaysia; the second from the small city of Kota Kinabalu; and the third from rural villages surrounding Kota Kinabalu. Groups differed in the BMI they considered most attractive, in that the more rural the population the higher the BMI they referred (Swami & Tovée, 2005a). For instance, the rural villagers found Caucasian female images with an average BMI of 23 kg/m² most attractive, while Kuala Lumpur residents preferred an average BMI of 21 kg/m² (Swami & Tovée, 2005a). Swami and Tovée (2007a) observed a similar but more pronounced trend in Thailand, where rural Thai men judged female Caucasian images with a BMI of 24 kg/m² most attractive, while Thai men living in Bangkok (the capital of Thailand) preferred a BMI of 21 kg/m² (Swami & Tovée, 2007a). Rural Thai men not only preferred a higher average BMI overall, they also judged heavy female images more positively than urban Thais (Swami & Tovée, 2007a). The difference in attractiveness preference between rural and urban populations were equally pronounced between indigenous Finnish men living in the most Northerly districts in Finland (25 kg/m²) and ethnic Finnish men living in Helsinki (21 kg/m²), the capital of Finland (Swami & Tovée, 2007). The indigenous Finnish men also viewed heavy bodies more positively than urban Finish men (Swami & Tovée, 2007). However, rural Samoan adolescent boys from the small Pacific island of Samoa, preferred the same BMI as their urban counterparts (21 kg/m², both groups) when judging female attractiveness of Caucasian images (Swami, Knight, et al., 2007). The rural adolescent boys did however view the heavier female bodies more positively than the urban boys (Swami, Knight, et al., 2007). A further study by Tovée et al (2006) examined the attractiveness preferences of Africans living in a rural area in South Africa, Africans that moved from South Africa to Britain in the 18 months prior to the study and Africans that were born and raised in Britain. All three groups differed significantly in the BMI they found most attractive, with rural South Africans preferring the highest BMI (27 kg/m²), British born Africans preferring the lowest BMI (21 kg/m²) and the African migrants preferring an intermediate BMI (24 kg/m²; Tovée, et al., 2006).

In general these studies show a definite trend for rural populations, where resources are comparatively scarce, to prefer heavier female bodies than urban populations. One problem with these studies, however, is that all of the cross-cultural studies (Swami, Antonakopoulos, et al., 2006; Swami, Knight, et al., 2007; Swami, Neto, et al., 2007; Swami & Tovée, 2005a; Swami & Tovée, 2007a; Swami & Tovée, 2007; Tovée, et al., 2006) seem to have used a single set of female Caucasian images, which

would limit the generality of the findings (particularly the consistent findings for urban populations) beyond the given image set. As discussed earlier, the ecological validity of using Caucasian images to test other ethnicities' attractiveness preferences is also debatable. Although it is often difficult to acquire images from different ethnicities, future research could benefit from using images from the same population as the observers.

Various different environmental, conditional, and cultural factors could explain the BMI preference differences between urban and rural populations. What is more, these factors are bound to be inter-related. For one, the optimal BMI for health and fertility might differ between different environments and racial groups (Tovée & Cornelissen, 2001), producing a difference in attractiveness preferences. Heavier individuals might be comparatively healthier in environments where there are low, or fluctuating, levels of resources because of the buffering effect of fat reserves. Since the mass media portrays a skinny ideal for female attractiveness (Garner, Garfinkel, Schwartz, & Thompson, 1980; Silverstein, Perdue, Peterson, & Kelly, 1986; Spitzer, Henderson, & Zivian, 1999; Tovée, Mason, Emery, McCluskey, & Cohen-Tovée, 1997; Wiseman, Gray, Mosimann, & Ahrens, 1992), and is comparatively more prevalent in urban environments, it is also possible that the media synchronizes (and lowers) BMI preferences in urban environments. Previous research has shown that men hungry for food (Swami & Tovée, 2006) and men who have a more 'restricted' sexual strategy (those who require a high emotional investment and prolonged courtship before engaging in sexual relations; Swami, et al., 2008) find heavier women more attractive than relatively more hunger satiated and 'unrestricted' men. Thus, conditional factors might also explain the preference for higher BMI individuals in rural populations. In section 1.7.4, I will discuss the role of environmental, conditional and cultural factors in attractiveness preferences in more detail.

If judgments of female attractiveness are based solely on perceptions of health, one might expect the optimum BMI for attractiveness and health to be similar. Tovée et al (2007) investigated perceptions of health and attractiveness in three groups of observers: British Caucasians, Africans living in a rural area in South Africa, and Africans that moved from South Africa to Britain in the 18 months prior to the study. Men and women from all three groups were asked to rate a set of Caucasian female images for health and attractiveness. The British Caucasian group showed virtually no difference between the

BMI they considered most healthy and most attractive, although the BMI they considered most healthy (21.1 kg/m^2) was slightly higher than the BMI they considered most attractive (20.9 kg/m^2 ; Tovée, et al., 2007). The difference between the optimum BMI for health and attractiveness was more pronounced in the two African groups. Both the Africans living in South Africa (RSA) and the African migrants preferred a moderately higher BMI for health (RSA: 30 kg/m^2 ; migrants: 26 kg/m^2) than for attractiveness (RSA: 27 kg/m^2 ; migrants: 24 kg/m^2 ; Tovée, et al., 2007). Swami et al (2008) found a similar preference difference for 'unrestricted' British men (those men willing to engage in sexual relations in the absence of commitment) judging female Caucasian images. These 'unrestricted men' also preferred very similar optimum BMIs for health and attractiveness, with a slight tendency to prefer a higher BMI for health (20.1 kg/m^2) than for attractiveness (19.9 kg/m^2 ; Swami, et al., 2008). Interestingly, men with a more 'restricted' sexual strategy showed a tendency in the opposite direction, preferring a slightly lower optimum BMI for health (21.4 kg/m^2) than for attractiveness (22.4 kg/m^2 ; Swami, et al., 2008). These results indicate that the BMI considered 'most healthy' and 'most attractive' are fairly closely aligned, although there are some indications that people differentiate between the most attractive and healthiest looking BMI. I will discuss this finding in more detail in Chapter 4 and 6, where I compare men and women's health and attractiveness preferences for optimum facial adiposity.

1.7.3.1.3.2. Male bodies

Compared to the vast amount of studies testing the association between body weight, shape and female attractiveness, relatively few studies have focused on male attractiveness. Singh (1995) designed a set of male line drawings consisting of four WHR levels (0.7-1.0) and three body weight levels (underweight, normal weight, overweight). Using this stimulus set they showed that Western female observers find a normal weight, WHR 0.9 figure most attractive (Singh, 1995). Using the same stimulus set, Furnham et al (1997) also found a preference for a WHR of 0.9 using a different group of male and female observers, while Henss (1995) showed no significant difference between the most attractive WHRs of 0.9 and 1.0. However, as mentioned previously, Henss' use of a between subjects design would have limited the statistical power of his study. Normal weight male figures were judged more attractive than both under-and-overweight figures in both the Furnham et al (1997) and Singh and Young (1995) studies.

In their pivotal study, Maisey, Vale, Cornelissen and Tovée (1999) tested the role of BMI, WHR and Waist-to-Chest Ratio (WCR) in male attractiveness by presenting unmodified colour images of male bodies to Western female observers. Individually all three measures were related to women's judgments of male attractiveness, but in the multiple-polynomial regression WCR was the principal determinant of attractiveness accounting for 56% of the variance; whereas BMI only accounted for 13% of the additional variance (Maisey, et al., 1999). WHR was not a significant predictor in the regression model. Women preferred men with comparatively more 'V-shaped' bodies (low WCRs), while also preferring an intermediate BMI of $\sim 22 \text{ kg/m}^2$, as opposed to under-or-overweight men (Maisey, et al., 1999). These results were replicated for British (Swami, et al., 2007; Swami & Tovée, 2005b), Greek (Swami, et al., 2007) and urban-Malaysian women (Swami & Tovée, 2005b). In all these studies WCR emerged as the principal, and BMI as a secondary, determinant of male attractiveness, while WHR did not contribute to the overall model (Swami, et al., 2007; Swami & Tovée, 2005b). Interestingly, rural Malaysian women based their attractiveness preferences primarily on BMI, with WCR playing a more minor role (Swami & Tovée, 2005b). Consistent with findings for female attractiveness, rural Malaysian women preferred a much higher BMI (24 kg/m^2) when judging male attractiveness than their urban counterparts, who preferred a similar BMI to British women (21 kg/m^2 , both groups; Swami & Tovée, 2005b). Rural Malaysian women also preferred a more tubular male body shape (high WCR), contrary to the 'V shaped' male bodies preferred by urban Malaysian and British women (low WCR; Swami & Tovée, 2005b).

Fan, Dai, Liu and Wu (2005) examined the role of WCR, BMI, WHR and the Volume-to-Height Index (VHI) in the attractiveness judgments of male 3D bodies by recruiting ethnic Chinese men and women from Hong Kong to judge a set of male Caucasian and Chinese bodies. Similar to previous studies they found that of the three standard anthropometrical measures (WCR, BMI and WHR), WCR was the strongest predictor of male attractiveness, followed by BMI (Fan, et al., 2005). However, VHI was more strongly related to male bodily attractiveness than any of the other measures, explaining 73% of the variance in male attractiveness (Fan, et al., 2005). This is an intriguing finding but one that should be treated with caution for the moment, as there were two major statistical problems with their study. First, Fan et al (2005) assumed a

linear relationship between the anthropometrical measures and male attractiveness in their analysis, which as discussed earlier would have disproportionately under estimated the role of WHR and BMI in attractiveness. Second, a closer inspection of their graphs reveals that the association between BMI and attractiveness is very different for Caucasian and Chinese images. The one group of images shows a curvilinear relationship, while the other shows a seemingly linear relationship. These two groups of images should therefore not have been combined in the analysis, but should instead have been analyzed separately. The relative importance of VHI in attractiveness therefore needs further verification.

In summary, although BMI (and percentage body fat) is closely associated with female attractiveness, BMI seems to play less of a role in male attractiveness. Nevertheless, BMI still remains a significant predictor of male attractiveness. The body mass index is determined by fat mass, lean mass (primarily muscle mass) and frame size (Garn, Leonard, & Hawthorne, 1986). Since men tend to have a fairly low percentage body fat (Meeuwssen, et al., in press), it follows that BMI is not an ideal indicator of male adiposity, except of course in overweight men with a very high percentage body fat. The predominance of WCR over BMI can be interpreted as a paramount female preference for muscularity, since men with a high WCR have more V-shaped bodies characteristic of body-builders. However, WCR should also be a good indicator of male adiposity as overweight men with the typical male pattern fat distribution should have more tubular bodies (low WCR). It follows that adiposity might also play an important role in male attractiveness, although one would expect a stronger influence of WHR on male attractiveness if adiposity was the principal determinant of male attractiveness. Studies using more sophisticated anthropometrical measures, such as bio-impedance measurements of percentage body fat and muscle, should be able to distinguish between the role of muscularity and adiposity in male attractiveness.

1.7.4. The role of environmental, conditional and cultural factors in attractiveness preferences

The ancient Greeks believed that 'beauty is in the eye of the beholder' noting that our ideas of attractiveness are not universal but differs from person to person. The standard contemporary view is that attractiveness preferences are near universal,

emerging early in development (Kissler & Bäumli, 2000; Langlois, et al., 1987; Langlois, Roggman, & Rieser-Danner, 1990) and generally shared across cultures (Cunningham, et al., 1995; Langlois, et al., 2000). As consideration of the complexity of human mate choice has increased, however, it has become clear that attractiveness preferences are influenced by a variety of factors. For instance, in earlier sections of this chapter we saw that various indices of a woman's condition (i.e. her own attractiveness, age, relationship status, conception risk etc.) affect her preference for masculinity in men's faces (e.g. Little, et al., 2001; Little, et al., 2002; Penton-Voak, et al., 1999). Not only that, but her preference for masculinity is also dependent on environmental factors (i.e. pathogen load, quality of her relationship with her family etc.; Boothroyd & Perrett, 2008; DeBruine, Jones, Crawford, et al., 2010; Penton-Voak, et al., 2004) and her sexual strategy (i.e. short term versus long term, fewer children versus more etc.; Little, et al., 2002; Moore, et al., 2009; Penton-Voak, et al., 1999). Similarly, both sexes' preferences for a partner's ideal body weight and shape differ not only between cultures, but also within cultures. As a general rule, the level of urbanization is associated with the ideal body weight of the prospective partner, with more urban observers preferring a lower body weight (Swami & Tovée, 2005a, 2005b; Tovée, et al., 2006; Yu & Shepard, 1998).

It is therefore clear that there are various factors that play a crucial role in what we find attractive. To date most studies have focused on factors that can be broadly defined as environmental and conditional factors, for example the pathogen load of the environment and observer age, respectively. It must be noted, however, that these factors are not mutually exclusive. For instance, in section 1.7.3.1.3.1 we saw that rural populations tend to prefer a heavier body weight compared to more urban populations (Swami & Tovée, 2005a, 2005b; Tovée, et al., 2006; Yu & Shepard, 1998). One could easily attribute a preference for a heavier body weight to the advantageous effect of fat reserves in a rural environment, where resources are expected to be low or more variable. However, one could also contend that people who live in a rural environment are exposed to a higher pathogen load, tend to be hungry more often and have a more 'restricted' sexual strategy, all of which have also been shown to increase the ideal weight for attractiveness (DeBruine, Jones, Crawford, et al., 2010; Penton-Voak, et al., 2004; Swami, et al., 2008; Swami & Tovée, 2006). Naturally all these factors are inter-related.

Attractiveness preferences may also vary depending on cultural factors (Symons, 1979). Culture constitutes “the totality of socially transmitted behavior patterns, arts, beliefs, institutions, and all other products of human work and thought”. Tooby and Cosmides (1992) distinguished between “transmitted” and “evoked” culture. Transmitted culture is the transfer of beliefs, values, norms etc., which occurs through social learning. Evoked culture refers to behavioural repertoires “evoked” by different social and environmental conditions (Gangestad, Haselton, & Buss, 2006; Tooby & Cosmides, 1992). The general tendency for populations in high pathogen load environments to develop a “culture of masculinity” with women preferring more masculine men (DeBruine, Jones, Crawford, et al., 2010; Penton-Voak, et al., 2004), might be interpreted as an example of “evoked culture”. Putting it simply, Tooby and Cosmides’ (1992) concept of evoked culture indicates a different route through which the ecological and social environment can influence individual behaviour. Instead of environmental influences acting on the individual directly, these influences act on the individual through their respective culture.

Tooby and Cosmides (1992) and Gangestad et al (2006) put a heavy emphasis on the role of evolved culture, arguably underestimating the role of transmitted culture. Even though some cross-cultural differences may be environmentally triggered without the mediation of cultural transmission, most of the behavioral differences between cultures cannot simply be evoked by interacting with the environment (Mameli, 2007). For example, although a woman in a high pathogen load environment might acquire a masculinity preference by consciously or subconsciously noticing that the masculine men just look a lot healthier than the others (evoked culture), the fact that most of the other women swoon at the sight of a masculine man (transmitted culture), might play an equally, if not more important role in the development of her masculinity preference.

Transmitted culture is also thought to be adaptive because it reduces the cost associated with individual learning. Cultural transmission usually occurs through social learning, in which an individual learns a new behaviour by watching other individuals perform the behaviour. Cultural learning allows us to acquire adaptive behaviors in an uncertain environment cheaply without costly individual learning by trial and error (Boyd & Richerson, 1985). It follows that cultural transmission is bound to play an important

adaptive role, allowing individuals to quickly and cheaply acquire knowledge and fine-tune their behaviour to local environments (Laland, 2007).

In summary, although our attractiveness preferences are universal at the most rudimentary level (i.e. most people worldwide would not find an open oozing sore attractive), there is a substantial amount of evidence indicating that our attractiveness preferences are mediated by environmental, conditional (and most likely cultural) information, allowing us to adjust our attractiveness preferences to our local conditions. The role of cultural, particularly mass media, influences in the mediation of attractiveness preferences will be discussed in more detail in chapters 4 and 6.

Chapter 2

Facial adiposity: a cue to health and attractiveness?

This chapter is based largely on work that was published in a peer-reviewed journal:

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Perception, 38, 1700–1711.

The version presented here is not the final print version.

2.1. Introduction

In the previous chapter I proposed that facial adiposity, or facial ‘fat’, might be an unacknowledged facial cue to health and attractiveness. Apart from being a valuable facial cue in itself, variation in facial adiposity might disrupt associations between other facial cues (such as symmetry, sexual dimorphism, averageness and skin condition) and judgements of attractiveness and health. Facial adiposity might also disrupt associations between other facial cues and actual health. For instance, as mentioned earlier, facial adiposity might conceal skeletal features, making it difficult to estimate symmetry accurately in overweight and obese individuals. Heavier individuals might therefore appear to be less symmetrical, not necessarily due to developmental instability but rather due to the measurement error introduced by facial adiposity. Indeed, Hume and Montgomerie (2001) did find an inverse association between BMI and facial symmetry, but whether this was due to increased developmental instability or the disruptive effect of facial adiposity remains to be seen.

In section 1.7.3.1, I provided several lines of evidence that support the notion that facial adiposity could be a valuable facial cue to health and attractiveness. First, Caucasian women, but not men, with a higher BMI are judged facially less attractive (Hume & Montgomerie, 2001; see discussion in section 1.7.3.1). Second, BMI, fat mass and lean mass are all highly heritable (Allison, et al., 1996; Forbes, et al., 1995; Schousboe, et al., 2010; Sorensen, et al., 1989; Stunkard, et al., 1990; Stunkard, et al., 1986), thus by choosing a partner with a ‘healthy’ weight, individuals can accrue indirect benefits for their offspring. Third, there is a substantial amount of evidence showing that the level of adiposity affects the health and survival ability of the individual, with both overweight and underweight individuals suffering negative fitness consequences (see discussion in section 1.7.3.1.2). Fourth, overall body weight, as measured by BMI and percentage body fat, is closely associated with female, and to some extent male, bodily attractiveness (see discussion in section 1.7.3.1.3). Taken together, these studies indicate that adiposity is a crucial predictor of health and attractiveness in bodies, especially in female bodies, and is therefore likely to be an important cue to health and attractiveness in the face.

The first aim of this study is to establish whether perceived facial adiposity serves as a cue to facial attractiveness, while the second is to test whether perceived facial adiposity serves as a valid cue to health. In order to be a valid cue, perceived facial adiposity must: (1) be used in the perception of health and (2) relate to actual health measures. We included systolic and diastolic blood pressure as measures of health, because of well-known association between excess weight and hypertension (Pi-Sunyer, 1993). We also included health measures specifically aimed at estimating the frequency and duration of infection, particularly respiratory infections. Several studies indicate a positive association between excess weight and respiratory infections. Obesity is associated with an increased risk of developing pneumonia in adults (Baik, et al., 2000) and overweight children are more likely to develop acute respiratory infections (Jedrychowski, et al., 1998; see discussion in section 1.7.3.1.2.4).

One plausible explanation for the association between excess weight and respiratory infections is the close association between excess weight and obstructive sleep apnoea (Salerno, et al., 2004; Wolk, Shamsuzzaman, & Somers, 2003; Young, Peppard, & Gottlieb, 2002), which increases the risk of pulmonary aspiration (Beal, et al., 2004). Since, lower respiratory track infections are normally initiated by the aspiration of small volumes of contaminated secretions from the upper respiratory tract (Johanson, 1984), increased pulmonary aspiration could produce a higher incidence of respiratory infections. Obstructive sleep apnoea is also associated with chronic inflammation of the upper and the lower respiratory tract (Antonopoulou, Loukides, Papatheodorou, Roussos, & Alchanatis, 2008; Carpagnano, et al., 2010; Rubinstein, 1995; Salerno, et al., 2004). This chronic inflammation of the respiratory tract might be partly due to the underlying systemic inflammation associated with obesity (Nieman, et al., 1999; Tanaka, et al., 1993; Visser, et al., 1999, 2001). Chronic inflammation is frequently accompanied by leucocytosis and a relative overproduction of immature (not fully developed) leucocytes (Abramson & Melton, 2000), most likely producing immune impairment. We also investigated how BMI relates to these groups of health measures in the study population.

2.2. Methods

This work was approved by the University of St Andrews Ethics Committee (Approval code: PS3137).

We recruited 42 female [Age: mean = 20.9, standard deviation (SD) = 1.05, range = 18–24; BMI: mean = 22.62, SD = 3.22, range = 17.82–31.51] and 41 male (Age: mean = 21.34, SD = 2.09, range = 18–27; BMI: mean = 23.28, SD = 2.75, range = 18.42–33.38) Caucasian participants from the University of St Andrews. All participants were photographed in front of a uniform Munsell 5 background, in full colour and under standard lighting conditions. Participants were seated a set distance from the camera, asked to maintain a neutral expression and had their hair pulled back. Each participant gave informed consent to take part in this study, was asked to complete a questionnaire and had their blood pressure, body weight and height measured. Questionnaires contained questions on gender, parental income (When you were growing up what was your household income?), respiratory diseases (How many times per year do you get a cold or flu?; How many days does one of your average cold and flu bouts last?) and antibiotics use (How many times did you take a course of antibiotics in the last year?). Systolic and diastolic blood pressures were measured twice with a Boots automatic blood pressure arm monitor (Boots Company PLC, England) after a minimum initial rest period of five minutes. Weight and height measures were used to calculate BMI [(weight in kilograms)/(height in metres)²] and BMI categories were assigned according to WHO criteria (World Health Organization, 2000).

The frequency and duration of cold and flu bouts are similar measures; we therefore included them in a principal component analysis (PCA), and identified one component with an eigenvalue > 1, which explained 62.51% of the variance in these two measures. Systolic and diastolic blood pressure were also included in a PCA, producing one component with an eigenvalue > 1. The blood pressure component explained 74.23% of the variance in these two measures. High values for these components indicate an increase in the frequency and duration of cold and flu bouts, and an increase in blood pressure, respectively.

Skewness and kurtosis values were low for all measures (skewness and kurtosis between –1.0 and 1.2), except for BMI (both sexes combined: kurtosis 1.4; male faces: kurtosis 3.5) and antibiotics use (skewness or kurtosis > 1.9 for both sexes, female faces and male faces). Log transformation did not sufficiently normalise the male BMI data (kurtosis 1.8) but the exclusion of one male participant with a BMI > 33 kg/m²

did (skewness and kurtosis between -0.1 and 0.1). The antibiotics use data were also not sufficiently normalised by log transformation (skewness or kurtosis > 1.9 for both sexes, female faces and male faces) because very few individuals reported using more than one course of antibiotics in the last year. We therefore grouped the antibiotics use data into three groups: high use (twice or more in the last year; $N = 8$), low use (once in the last year; $N = 34$) and zero use (zero use in the last year; $N = 13$) for the combined analysis of both sexes. For the single sex analyses, the sample sizes for each of the three antibiotics use groups were unbalanced. We therefore did a median split for each sex, producing a high and low antibiotics use category for male (high: $N = 19$; low: $N = 13$) and female faces (high: $N = 16$; low: $N = 5$). Antibiotics use in the combined male and female data set was subsequently analysed using a Kruskal Wallis test followed by Mann-Whitney tests to compare the three groups. In the single sex analyses we compared antibiotics use between the high and low groups with Mann-Whitney tests. All other relationships between health measures, facial adiposity and BMI were tested using Pearson's correlations. Data were missing for cold and flu component (1 participant), parental income (2 participants), antibiotics use (29 participants) and blood pressure component (1 participant).

Images were resized (female images: 387×478 pixels; male images: 389×518 pixels), colour corrected ($\Delta E = 2.44$) using in-house software and standardised for inter-pupillary distance and position using PsychoMorph version 8.4.7.0. We recruited four groups of participants to rate the facial images for health, attractiveness and weight. First, 26 Caucasian participants (12 female, 14 male; mean age = 22.81, SD = 2.02, range = 18–28) rated each female image for health and attractiveness on a seven-point Likert scale (0 = very unhealthy/unattractive; 3 = average; 6 = very healthy/attractive). Second, 22 Caucasian participants (12 female, 10 male; mean age = 21.87, SD = 2.25, range = 18–26) rated each male image for health and attractiveness on the same scale. Third, 26 Caucasian participants (14 female, 12 male; mean age = 20.81, SD = 2.36, range = 20–28) rated each female facial image for weight on a seven-point Likert scale (0 = very underweight; 3 = average weight; 6 = very overweight). Lastly, 29 Caucasian participants (17 female, 12 male; mean age = 21.1, SD = 2.87, range = 19–26) rated each male facial image for weight on the same scale. In all four studies, participants were shown all the images before rating commenced to make them aware of the range and variability of the images. Images were presented in a randomised order

and participants were asked to indicate whether or not they knew the person. Perceived weight ratings were used as a measure of perceived facial adiposity.

We recorded the time it took the participants to rate each image and excluded all participants with an average time of less than 1.65 seconds per question, for two or more images (Group 1: 5 participants; Group 2: 1 participant; Group 3: 3 participants; Group 4: 4 participants). The threshold value was defined by the maximum time it took the experimenter to select random answers as quickly as possible and included submission time. We also removed rating data if the participant knew the rated individual (Group 1: 9.6% of ratings; Group 2: 5.9% of ratings; Group 3: 5.8% of ratings; Group 4: 4.8% of ratings). Facial health ($p = 0.62$), attractiveness ($p = 0.75$) and weight ratings ($p = 0.22$) did not differ significantly between male and female raters (independent samples t-test). Data from both sexes were therefore combined for analysis. Inter-rater reliability was very high for facial health (Cronbach $\alpha = 0.87$), facial attractiveness ($\alpha = 0.92$) and facial adiposity ($\alpha = 0.84$). Given the consistency of ratings, the scores were averaged across participants for each of the 84 images. Skewness and kurtosis values were low for all three measures ($-0.86 > \text{skewness}$ and $\text{kurtosis} < 0.35$).

2.3. Results

2.3.1. Perceived facial adiposity and BMI.

Despite the fact that a significant relationship between perceived facial adiposity and BMI might seem evident, we wanted to examine the strength of this relationship. To do so we fitted a General Linear Model (GLM) in SPSS version 16 to test if participants' judgement of weight using facial images related to measured body weight. BMI significantly and positively predicted perceived facial adiposity for male and female faces combined ($F_{1,80} = 61.02$; $p \leq 0.0005$, $R^2 = 0.43$; Figure 1), for female faces only ($F_{1,40} = 31.87$; $p \leq 0.0005$, $R^2 = 0.44$) and for male faces only ($F_{1,38} = 34.18$; $p \leq 0.0005$, $R^2 = 0.47$).

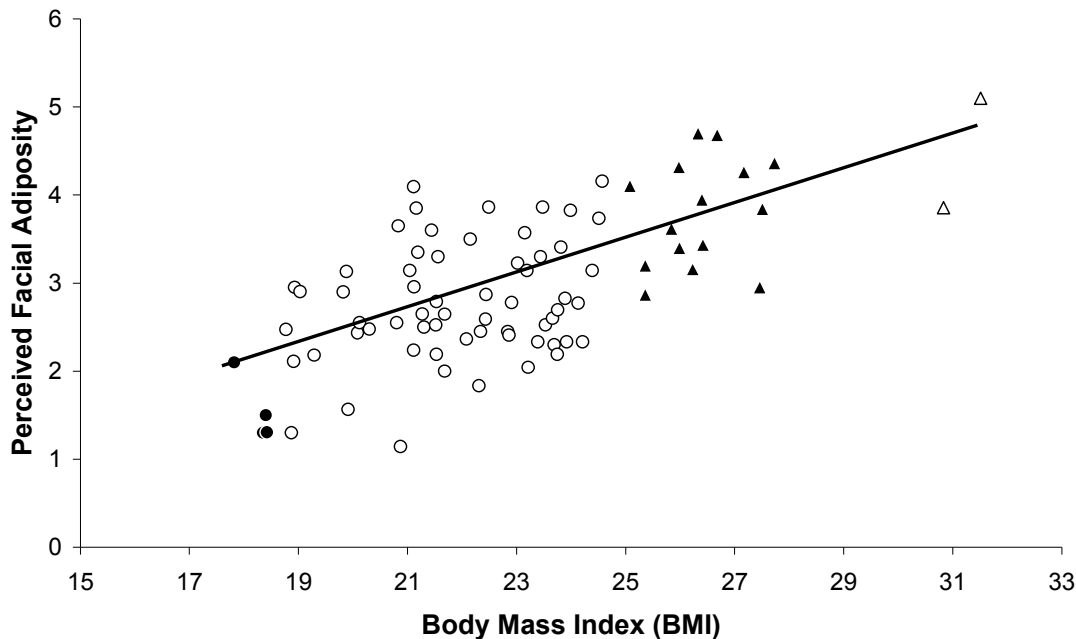


Figure 2: Interrelation between perceived facial adiposity and body mass index.

Heavier individuals are consistently judged to have a higher facial adiposity throughout the BMI spectrum: underweight (solid circles), normal weight (open circles), overweight (solid triangles), and obese (open triangles). The continuous line gives the best-fit General Linear Model.

2.3.2. Perceived facial adiposity, health and attractiveness

We fitted a multiple polynomial GLM to test the relationship between perceived facial adiposity, health and attractiveness. Second order equations were included since both underweight and obese individuals should be rated less healthy and attractive. The following polynomial model was fitted for both health and attractiveness judgements: Model: $y = a + b_1x + b_2x^2 + e$, where y is the health or attractiveness rating, a is the intercept, b_1 and b_2 are coefficients, x is perceived facial adiposity and e is the random error. The quadratic model significantly predicted perceived health ($F_{2,39} = 11.26$; $p \leq 0.0005$, $R^2 = 0.37$; Figure 2) and perceived attractiveness ($F_{2,39} = 7.27$; $p = 0.002$, $R^2 = 0.27$; Figure 2) in female faces. The quadratic model also significantly predicted perceived health ($F_{2,37} = 5.86$; $p = 0.006$, $R^2 = 0.24$; Figure 3) and perceived attractiveness ($F_{2,37} = 6.81$; $p = 0.003$, $R^2 = 0.27$; Figure 3) in male faces. It is interesting

to note that compared to men at the low end of the perceived facial adiposity spectrum, women at the low end of the spectrum seem to be judged less harshly, especially in terms of attractiveness.

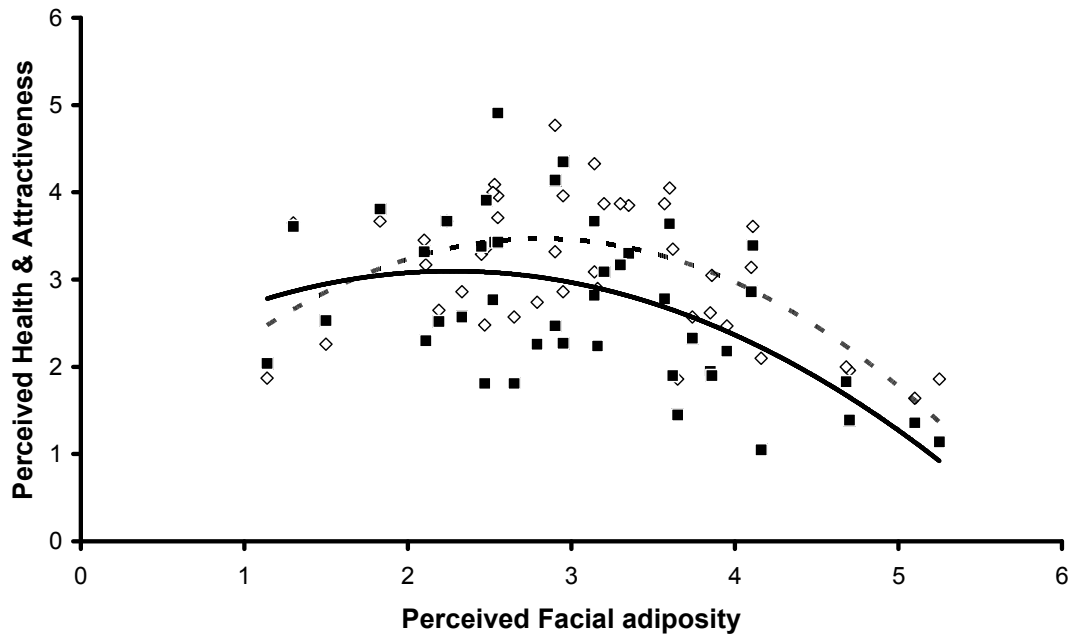


Figure 3. The relationship between facial adiposity health and attractiveness judgements in female faces. Women with an intermediate perceived facial adiposity are judged healthier and more attractive than women with a perceived facial adiposity on either side of these optima. Solid squares and the solid curve indicate attractiveness judgements, while open diamonds and the dashed line indicate health judgements. Interestingly, the optimum perceived facial adiposity for attractiveness is lower than the optimum facial adiposity for health.

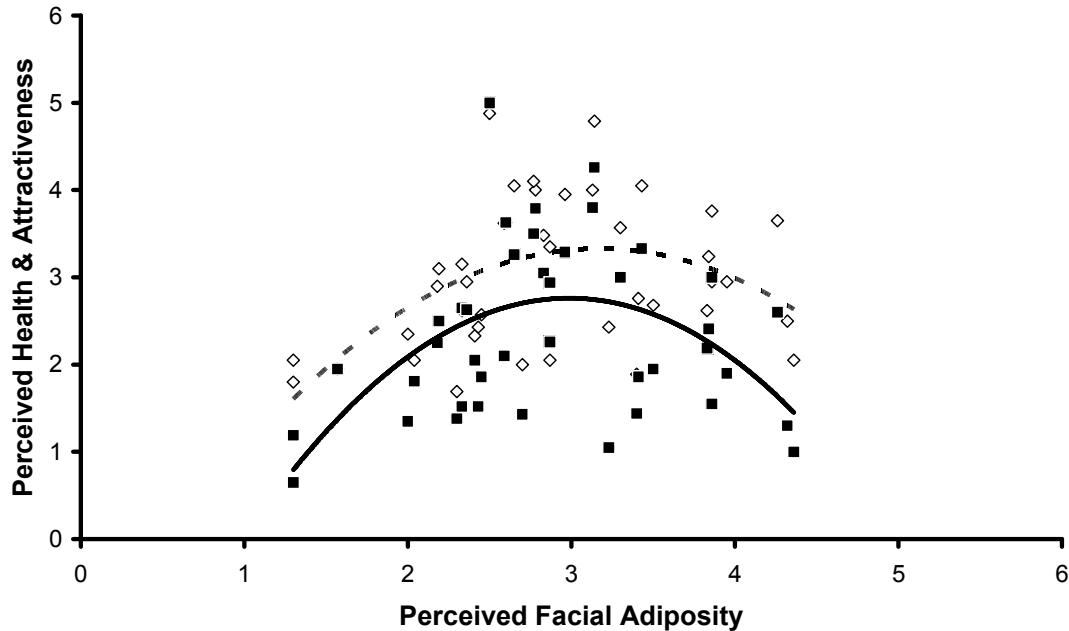


Figure 3: The relationship between facial adiposity, health and attractiveness judgements in male faces. Men with an intermediate perceived facial adiposity are judged healthier and more attractive than men with a perceived facial adiposity on either side of these optima. Solid squares and the solid curve indicate attractiveness judgements, while open diamonds and the dashed line indicate health judgements. Similar to the female faces, the optimum perceived facial adiposity for attractiveness is also lower than the optimum facial adiposity for health.

Exploration of the relationship between perceived facial adiposity and both perceived health and attractiveness showed that other regression models based on linear, logarithmic, inverse, compound, power, S, growth, exponential and logistic functions did not fit the data significantly. Cubic models also fitted the perceived health (Female faces: $F_{3,38} = 7.32$, $p = 0.001$, $R^2 = 0.37$; Male faces: $F_{3,36} = 3.94$, $p = 0.016$, $R^2 = 0.25$) and attractiveness (Female faces: $F_{3,38} = 4.91$, $p = 0.006$, $R^2 = 0.28$; Male faces: $F_{3,36} = 4.49$, $p = 0.009$, $R^2 = 0.27$) data well, but we consider the quadratic models more appropriate for two reasons. First, because R^2 increases with the number of regressors in the model, higher order models tend to have inflated R^2 values. Second, the cubic fit is very close to the quadratic fit in all cases (health and attractiveness judgements; male and female faces; see example for attractiveness judgements in Figure 4).

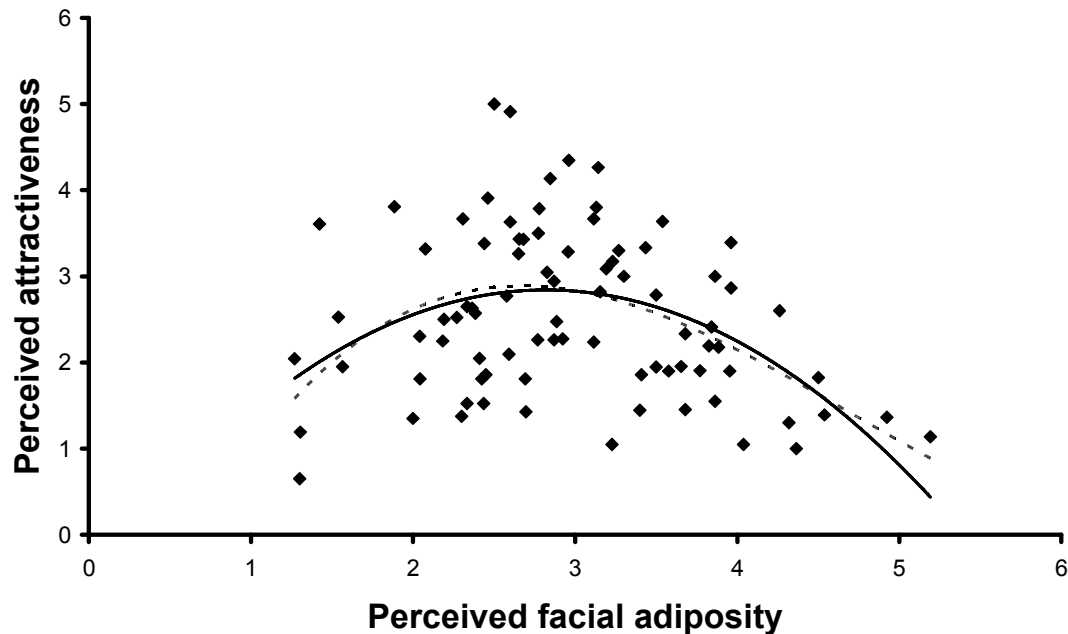


Figure 4: Interrelation between facial adiposity and facial attractiveness judgements in both sexes. The solid curve is the best-fit 2nd order polynomial equation. The 3rd order (cubic) polynomial equation is indicated as a dashed line. Both curves are very similar.

2.3.3. Calculating equivalent BMI values for perceived facial adiposity optima

Perceived facial adiposity optima were estimated from figures 2 and 3 (after increasing the sensitivity of the scale on the x-axis to 0.1 units). We used GLM parameter estimates to determine the linear relationship between BMI and perceived facial adiposity. The linear relationship for female faces was $y = 15.440 + 2.367x$, and for male faces $y = 16.406 + 2.384x$, where y is BMI and x perceived facial adiposity. Using these formulas I calculated the equivalent BMI values of the perceived facial adiposity optima, namely female attractiveness (20.9 kg/m²), female health (22.1 kg/m²), male attractiveness (23.6 kg/m²) and male health (24.0 kg/m²). For both male and female faces, the most attractive equivalent BMI was lower than the healthiest looking equivalent BMI.

2.3.4. Perceived facial adiposity and health measures

To test the relationship between perceived facial adiposity and actual health, we performed separate zero-order and partial Pearson's correlations (all two-tailed). In the partial correlations we partialled out age and parental income. Age is a determining factor of facial adiposity (Rohrich, Pessa, & Ristow, 2008). Socio-economic status is widely reported as a covariate of health and we therefore controlled for parental income, as a limited measure of socio-economic status. We report the partial correlations, although the zero-order correlations were similar (see Table 1). The cold and flu component was significantly and positively correlated with perceived facial adiposity ($r_{74} = 0.30$, $p = 0.008$; Table 1). To test whether perceived facial adiposity was significantly associated with the cold and flu component in both sexes, we also performed separate correlations for male and female faces. The cold and flu component was significantly correlated with perceived facial adiposity in male faces ($r_{35} = 0.35$, $p = 0.036$) and tended to be correlated with perceived facial adiposity in female faces ($r_{35} = 0.32$, $p = 0.052$; Table 1). In the combined analysis of male and female faces, antibiotics use was significantly associated with perceived facial adiposity (Kruskal Wallis $\chi^2 = 9.71$, $df = 2$, $p = 0.008$; Table 1). Facial images of individuals who reported high antibiotics use were judged significantly heavier than those who reported low antibiotics use (Mann Whitney $U = 46.00$, $p = 0.012$) and those that reported zero use ($U = 10.50$, $p = 0.003$). There was no significant difference in perceived facial adiposity between low use and zero use individuals ($U = 150.50$, $p > 0.1$). In the single sex analyses, antibiotics use was significantly associated with perceived facial adiposity in female ($U = 14.00$, $p = 0.032$) but not in male faces ($U = 85.50$, $p > 0.1$). The blood pressure component significantly and positively correlated with perceived facial adiposity when both sexes were combined ($r_{74} = 0.36$, $p = 0.001$) and in female faces ($r_{35} = 0.48$, $p = 0.003$), but only tended to be correlated in male faces. ($r_{35} = 0.31$, $p = 0.066$; Table 1).

Table 1. Pearson's correlations showing the relationship between perceived facial adiposity, BMI and actual health measures. Partial correlations controlled for parental income and age. All correlations were two-tailed. Associations with antibiotics use were tested using a Kruskal Wallis test for the combined male and female faces, and Mann-Whitney tests for the single sex associations.

	Facial adiposity		BMI	
	Zero-order r (df)	Partial r (df)	Zero-order r (df)	Partial r (df)
Both sexes				
Cold & Flu component	0.29** (81)	0.30** (74)	0.24* (81)	0.26* (74)
Antibiotics use	$\chi^2 = 9.71^{**} (2)$		$\chi^2 = 9.52^{**} (2)$	
Blood pressure component	0.40*** (81)	0.36** (74)	0.48*** (81)	0.45*** (74)
Female faces				
Cold & Flu component	0.31* (41)	0.32 ^Φ (35)	0.34* (41)	0.37 ^Φ (35)
Antibiotics use	$U=14.00^* (20)$		$U=13.00^* (20)$	
Blood pressure component	0.53*** (41)	0.48** (35)	0.60*** (41)	0.60*** (35)
Male faces				
Cold & Flu component	0.27 ^Φ (40)	0.35* (35)	0.16 (40)	0.22 (35)
Antibiotics use	$U=85.50 (31)$		$U=77.00^{\Phi} (31)$	
Blood pressure component	0.37* (40)	0.31 ^Φ (35)	0.34* (40)	0.40* (35)

*** $p \leq 0.001$, ** $p \leq 0.01$, * $p \leq 0.05$, ^Φ $p \leq 0.10$.

2.3.5. BMI and health measures

If perceived facial adiposity is accurately displaying relative body weight, one might expect perceived facial adiposity and BMI to correlate with health measures in a similar way. To test this we performed zero-order and partial Pearson's correlations controlling for parental income and age. Results for BMI were fairly similar to those obtained for perceived facial adiposity (Table 1). The cold and flu component correlated significantly with BMI for male and female faces combined ($r_{74} = 0.26$, $p = 0.022$;) and for female faces ($r_{35} = 0.37$, $p = 0.024$), but not for male faces ($r_{35} = 0.22$, $p > 0.1$; Table 1). In the combined analysis of male and female faces, antibiotics use was significantly associated with BMI (Kruskal Wallis $\chi^2 = 9.52$, $df = 2$, $p = 0.009$; Table 1). Individuals who reported high antibiotics use were significantly heavier than those who reported low antibiotics use (Mann Whitney $U = 43.00$, $p = 0.008$) and those that reported zero use ($U = 9.00$, $p = 0.002$), while there was no significant difference in BMI between low use and zero use individuals ($U = 166.00$, $p > 0.1$). In the single sex analyses, BMI was positively associated with antibiotics use in female ($U = 13.00$, $p = 0.025$) but only tended to be associated with antibiotics use in male faces ($U = 77.00$, $p = 0.077$). Male and female individuals with higher BMIs had significantly higher blood pressure ($r_{74} = 0.45$, $p \leq 0.0005$; Table 1). The correlation between the blood pressure component and BMI remained significant when female ($r_{35} = 0.60$, $p \leq 0.0005$) and male faces ($r_{35} = 0.40$, $p = 0.015$; Table 1) were analysed separately.

2.4. Discussion

This study set out to test whether facial adiposity is a cue to health and attractiveness. As expected, people are quite accurate at judging weight based on facial cues alone, enabling facial adiposity to serve as a potential cue to health and attractiveness. In order to be a valid cue to health, any cue must fulfil two prerequisites. First, people must use this cue in their judgements of health. Second, this cue must be associated with actual health measurements. Both criteria were met in the results. We present evidence that people use perceived facial adiposity as a cue when judging health in both male and female faces. Adiposity produces a fairly salient shape cue in the face, so it is parsimonious to assume that facial adiposity, rather than a correlate thereof, provides the basis for estimating health (in chapter 3 we identify three such salient shape

cues). Men and women with intermediate facial adiposity are judged healthier than individuals with a facial adiposity on either side of this optimum. Weight is an extremely important cue to perceived health in bodies, especially in female bodies (see discussion in section 1.7.3.1.3). Swami et al (2008) and Tovée et al (2007) showed that BMI explains between 77 and 82 % of the variance in health judgements of female Caucasian bodies. We show that this is also true for the face, although perceived facial adiposity explains only 37% of the variance in health judgements in female faces and 24% of the variance in male faces. This discrepancy in the amount of variance explained is not surprising given that there is a whole range of putative facial cues such as symmetry, averageness, sexual dimorphism and skin condition that also signal health.

Furthermore, we show that perceived facial adiposity provides information about past health and probable future health. Individuals with high perceived facial adiposity report significantly more infections than those with low perceived facial adiposity. These apparently high weight individuals report a significantly higher frequency of antibiotics use and longer and more frequent respiratory infections. Despite the smaller sample size in the single face sex analyses, the association between perceived facial adiposity and infection is significant or tend to be significant in both male and female faces (except for the association between male facial adiposity and antibiotic use which did not reach significance).

We also show a strong association between perceived facial adiposity and cardiovascular health. Individuals with higher perceived facial adiposity have significantly higher blood pressure, a condition that increases their risk of coronary heart disease and stroke (MacMahon, et al., 1990). One might argue that cardiovascular disease did not play an important role in shaping the mate preferences of our ancestors. Yet, cardiovascular disease is currently an enormous health burden in the developed world (World Health Organization, 2003). It is therefore plausible that current mate choice preferences are shaped by the environment the individual finds it self in. People change their preferences according to their local environment (e.g. Furnham, Moutafi, & Baguma, 2002; Sugiyama, 2004; Swami & Tovée, 2005a, 2005b; Tovée, et al., 2006; Yu & Shepard, 1998). For instance, people in rural areas, where food can be scarce, find heavier women more attractive than people in urban areas (Swami & Tovée, 2005a; Swami & Tovée, 2007a; Swami & Tovée, 2007; Tovée, et al., 2006). Preferences can

also change rapidly (e.g. Swami & Tovée, 2006; Tovée, et al., 2006), so it is probable that modern humans are associating excess weight and obesity with negative health outcomes. Interestingly, we observed that perceived facial adiposity is more strongly associated with blood pressure in women than in men. This sex difference could potentially be attributed to the fact that for a given weight women tend to have a higher percentage body fat than men (Meeuwsen, et al., in press). Thus, the women with a high degree of facial adiposity in our study would have a higher percentage body fat than their counterpart men and may therefore have been driving the association between blood pressure and perceived facial adiposity.

The association between these actual health measures and BMI are fairly similar to those observed for perceived facial adiposity, further strengthening the observed effect between perceived facial adiposity and the actual health measures. It is interesting to note, however, that all three actual health measures (e.g. respiratory infections, antibiotics use and blood pressure) is more strongly associated with BMI in women than in men. This could probably be attributed to the fact that BMI is a relatively poor measure of adiposity in men (see discussion in section 1.7.3.1.3.2).

Not only is perceived facial adiposity (or a correlate thereof) used as a cue to health, it is also a powerful correlate of attractiveness. Men and women with intermediate perceived facial adiposity are judged more attractive than individuals with high and low perceived facial adiposity. Interestingly, while men with a low degree of facial adiposity are judged much less attractive than men with an intermediate level of facial adiposity, women at the low end of the facial adiposity spectrum are judged comparatively less harshly. Furthermore, this sex difference is more pronounced for attractiveness than for health judgements. One plausible explanation for this finding is that the Western media's portrayal of a skinny female ideal (Garner, et al., 1980; Silverstein, et al., 1986; Spitzer, et al., 1999; Tovée, et al., 1997; Wiseman, et al., 1992), might have altered people's perceptions of the 'most attractive' female weight, while leaving health judgements relative untouched. Consistent with this explanation, we found a large difference between the 'most attractive' and 'most healthy' looking equivalent BMI in female faces (1.2 kg/m^2), with only a small difference in male faces (0.4 kg/m^2). In both male and female faces the equivalent BMI optimum for health was higher than the BMI optimum for attractiveness. I will explore this concept further in chapters 3,4, 5 and 6.

In general the equivalent BMI values estimated using the perceived facial adiposity optima, were fairly consistent with work done in bodies, validating our use of a perceived measure of facial adiposity and verifying that people can accurately judge weight from the face. For instance, in female faces the equivalent BMI for attractiveness was 21 kg/m², closely aligned with BMI optima obtained from work on female bodies in the British population (19–21 kg/m²; Swami, Antonakopoulos, et al., 2006; Swami, Knight, et al., 2007; Swami, Neto, et al., 2007; Swami & Tovée, 2005a; Tovée, et al., 2000; Tovée, et al., 1998; Tovée, et al., 2006). The equivalent optimum BMI for apparent health in female faces (22 kg/m²) was slightly higher than the optimum BMI observed for apparent health in female bodies (20–21 kg/m²; Swami, et al., 2008; Tovée, et al., 2007), as was the equivalent optimum BMI for attractiveness in male faces (24 kg/m²), compared to male bodies (21–22 kg/m²; Maisey, et al., 1999; Swami & Tovée, 2005b). To our knowledge, our study is the first to determine the optimum BMI for apparent male health (24 kg/m²) in either faces or bodies.

In summary, we set out to test the hypothesis that facial adiposity can act as a cue to health. We showed that perceived facial adiposity significantly predicts health and attractiveness in a Western population and is associated with actual health risk in the same population. Perceived facial adiposity explains a substantial amount of the variance of perceived health and attractiveness, thus studies focusing on other facial cues (e.g. symmetry, sexual dimorphism, averageness etc.) could benefit from controlling for facial adiposity. For example, the association between facial symmetry and health may be strengthened by controlling for facial adiposity. Our study provides one route through which facial characteristics can provide an accurate reflection of health, and thereby influence mate choice.

Chapter 3

Deciphering faces: Quantifiable visual cues to weight.

This chapter is based largely on work that was published in a peer-reviewed journal:

Coetzee, V., Chen, J., Perrett, D. I. & Stephen, I. D. (2010) Deciphering faces: quantifiable visual cues to weight. *Perception*, 39, 51–61.

The version presented here is not the final print version.

3.1. Introduction

In the previous chapter, we identified perceived facial adiposity as a novel facial cue to attractiveness and also a valid cue to health. We showed that perceived facial adiposity in young adults is significantly associated with both perceived and actual health, as measured by respiratory infections, antibiotics use and blood pressure (Coetzee, Perrett, & Stephen, 2009). We also showed that people are fairly accurate at judging weight based on facial cues alone, with BMI explaining between 44% and 47% of the variance in facial adiposity judgements (Coetzee, et al., 2009; see also previous chapter).

The question now remains, what are the proximate facial cues people use to judge weight? We specifically want to identify quantifiable facial cues to weight that are available in images. Throughout this study, weight is defined as weight scaled for height and measured by the body mass index (BMI). BMI is a widely used measure of weight, and is significantly related to female bodily attractiveness (e.g. Swami, Neto, et al., 2007; Swami & Tovée, 2005a; Thornhill & Grammer, 1999; Tovée, et al., 1998; Tovée, et al., 2006), and to some extent male bodily attractiveness (e.g. Maisey, et al., 1999; Swami, et al., 2007; Swami & Tovée, 2005b; see discussion in section 1.7.3.1.3). In addition, BMI is closely related to health (e.g. Balkau, et al., 2007; Pi-Sunyer, 1993; Willett, et al., 1995) and reproductive potential (Ellison, 2003; Frisch, 1987; Nguyen, Wilcox, Skjaerven, & Baird, 2007; Zaadstra, et al., 1993) in both sexes (see discussion in section 1.7.3.1.2). Three components contribute to BMI: fat mass, lean mass (mostly muscle mass) and frame size (Garn, et al., 1986).

Identifying any quantifiable cue in a 2D facial image can be a formidable task. Potential visual cues in 2D images are always limited, especially for weight which is essentially volumetric in nature. These limitations are amplified in the face because of the localised nature of fat distribution. A large percentage of the facial fat is localised in the buccal fat pads located in the cheek (Kahn, Wofram-Gabel, & Bourjat, 2000; Tostevin & Ellis, 1995). Despite these constraints in 2D faces, it should be possible to find quantifiable visual cues for weight, since weight is readily perceived.

Perimeter-To-Area Ratio

Previous literature offers several viable candidate cues for measuring weight in the face. Tovée et al (1999) identified the perimeter-to-area ratio as an accurate, quantifiable, cue for BMI in female bodies. They measured the perimeter-to-area ratio of 2D female bodies (excluding the head), in front view, and found that the perimeter-to-area ratio explained more than 70% of the variance in BMI (Tovée, et al., 1999). The effect of weight on perimeter-to-area ratio can be visualised as follows: a perfectly round circle has the smallest perimeter for a given area of any 2D shape, therefore the lowest possible perimeter-to-area ratio. Similarly, as the body increases in volume with excess weight, the area increases more than the perimeter, decreasing the perimeter-to-area ratio. Tovée et al (1999) also tested the association between BMI and 11 parallel width measures distributed evenly across the length of the torso. Most of the width measures, especially the waist width, showed a significant association with BMI in female bodies (Tovée, et al., 1999).

Check-to-Jaw Width

One of the most widely used facial relative width measures is cheekbone prominence. Cunningham et al (1990) defined cheekbone prominence as the difference between the width of the face at the cheekbones (cheekbone width) and the width of the face at the mouth (jaw width), divided by the length of the face. They showed a significant correlation between cheekbone prominence and attractiveness in three male Caucasian populations. A later study by Scheib et al (1999) simplified the measure of cheekbone prominence to cheekbone width divided by jaw width. They did not report individual correlates of cheekbone prominence, but instead combined cheekbone prominence with lower face length to produce a masculinity index. This masculinity index correlated significantly with attractiveness and symmetry in male faces (Scheib, et al., 1999). Facial measures of sexual dimorphism could be related to BMI as sex hormones influence fat, muscle and bone ratios (Blouin, Boivin, & Tchernof, 2008; Malina, 2005). Penton-Voak et al (2001) used the same measure as Scheib et al (1999) to measure cheekbone prominence in both males and females, but did not find a significant association between cheekbone prominence, symmetry and attractiveness in males. Crucially, however, they noticed that cheekbone prominence is smaller (i.e. less prominent) in males than in females (Penton-Voak, et al., 2001). This is not to say that men do not have wider cheekbones than women. On an absolute scale, adult men do have wider cheekbones than adult women (Enlow & Hans, 1996; Weston, Friday, & Lia, 2007). Cheekbone

prominence, as defined by (Scheib, et al., 1999), is a ratio measure that calculates the ratio of cheekbone width to jaw width. Jaw width itself is a sexually dimorphic feature as adult men have wider jaws than adult women even after controlling for allometric differences in face size (Gangestad & Thornhill, 2003; Thornhill & Gangestad, 2006). Thus, in essence, cheekbone prominence as defined by Scheib et al (1999) is more an inverse measure of how square the face is than cheekbone prominence *per se*. A smaller ratio would therefore indicate a squarer face (i.e. smaller difference between cheekbone width and jaw width) than a larger ratio.

Width-To-Height Ratio

Another relative width measure frequently mentioned in the literature on faces is width-to-height ratio. Penton-Voak et al (2001) defined the facial width-to-height ratio as the cheekbone width divided by the lower face height (vertical distance between the outer corner of the eye and the bottom of the chin). In their study, the width-to-height ratio did not correlate significantly with symmetry or attractiveness in male faces but was significantly different between the sexes. Women had significantly larger width-to-height ratios than men (Penton-Voak, et al., 2001). Gangestad and Thornhill (2003) adapted the width-to-height ratio by dividing the cheekbone width by the vertical distance between the hairline and the bottom of chin. They did not find a significant difference in this measure between the sexes (Gangestad & Thornhill, 2003). The two studies differed not only in their measure of facial height, but also their sample sizes, ethnicities, age range and standardisation methods. In both studies the height measure included the entire lower face (including the lower jaw). Since men have significantly longer lower jaws than women (Enlow & Hans, 1996; Gangestad & Thornhill, 2003; Thornhill & Gangestad, 2006), the height measure cannot be used to standardise cheek width.

In a recent study, Weston et al (2007) described a new width-to-height ratio from the morphometric analysis of hominin skulls. They defined the ratio as the cheekbone width divided by the upper face height (distance between the nasion and the prosthion; (Weston, et al., 2007). This upper face region can be roughly envisioned as the distance between the upper eyelids and the most superior point of the upper lip. Unlike the lower jaw region, the upper face region is not sexually dimorphic (Enlow & Hans, 1996; Weston, et al., 2007) and can therefore be used to standardise cheekbone width, thus providing a method of measuring relative cheekbone width (i.e. cheekbone width scaled for absolute

size). Weston et al (2007) showed a significant difference in the width-to-height ratio between the sexes, indicating that men have significantly wider faces than women after controlling for upper face height. A later study by Carre´ and McCormick (2008) adapted the facial width-to-height ratio for use in 2D facial photographs. Due to the difficulty in identifying the prosthion and nasion in real facial photographs, they changed the upper facial height used by Weston et al (2007) to the distance between the most superior point of the upper lip and the most inferior point of the eyebrow. Carre´ and McCormick (2008) found that men had a significantly larger facial width-to-height ratio compared with women, and that men with a high facial width-to-height ratio were relatively more dominant and aggressive than their low width-to-height ratio counterparts. However, a recent study by (Pound, et al., 2010), did not find a significant gender difference in the facial width-to-height ratio.

The aim of study 1 is to test whether three quantitative cues (perimeter-to area ratio, width-to-height ratio and cheek-to-jaw width ratio) relate to body weight (as measured by BMI). To test the universality of the relationship between these three quantitative visual cues and BMI we use both Caucasian and African images. We propose that the perimeter-to-area ratio will be inversely related to BMI, as both the buccal fat volume and the muscle volume (specifically masseter muscle volume) increase with increased weight. The cheek-to-jaw width ratio should also inversely relate to BMI, as the increased buccal fat and masseter muscle volume should also increase the jaw width. The width-to-height ratio should increase along with BMI, as heavier individuals should also have a bigger frame size. In study 2 we want to test if these quantifiable cues relate to perceived facial adiposity.

3.2. Study 1: Quantifiable facial cues for weight

3.2.1. Methods

The University of St Andrews ethics committee approved the study on Caucasian data set A (Approval code: PS3137) and B (Approved: Cornwell et al. 21 January 2004). African study A was approved by the ethics committees of the University of Pretoria (Approval code: EC 030606-018) and the University of the Witwatersrand (Approval code: M03-06-07), while African study B was approved by the University of St. Andrews ethics

committee (Approval code: PS5199) and the University of Pretoria ethics committee (Approval code: EC090304-020).

3.2.1.1. Materials

Caucasian data set A

We recruited 43 female (Age: mean = 20.9, SD = 1.04, range = 18–24; BMI: mean = 22.6, SD = 3.22, range = 17.8–31.5) and 41 male (Age: mean = 21.3, SD = 2.09, range = 18–27; BMI: mean = 23.3, SD = 2.75, range = 18.4–33.4) Caucasian participants from the University of St Andrews, Scotland.

Caucasian data set B

We recruited 52 female (Age: mean = 19.9, SD = 1.31, range = 18–22; BMI: mean = 22.3, SD = 2.55, range = 17.9–30.5) and 54 male (Age: mean = 20.4, SD = 1.57, range = 18–24; BMI: mean = 23.4, SD = 2.71, range = 18.1–30.0) Caucasian participants from the University of St Andrews. The male participants were recruited at two different time points (first: 30 males; second: 24 males).

African data set A

We recruited 51 female (Age: mean = 19.8, SD = 1.59, range = 18–26; BMI: mean = 22.1, SD = 5.01, range = 16.3–37.6) and 45 male (Age: mean = 21.2, SD = 2.20, range = 18–26; BMI: mean = 20.0, SD = 2.79, range = 16.4–29.4) African participants from the University of Pretoria and the University of the Witwatersrand, South Africa.

African data set B

We recruited 48 female (Age: mean = 19.6, SD = 1.91, range = 18–24; BMI: mean = 24.3, SD = 6.19, range = 17.4–40.0) and 47 male (Age: mean = 19.9, SD = 2.37, range = 18–29; BMI: mean = 20.9, SD = 2.99, range = 15.9–28.1) African participants from the University of Pretoria.

3.2.1.2. Procedure

All data sets

The four data sets were collected at different time points under slightly different conditions. We took facial photographs of all the participants in full colour and under standard lighting conditions. Participants were seated a set distance from the camera, asked to maintain a neutral expression and had their hair pulled back. Each participant gave informed consent to take part in this study, completed a questionnaire containing questions on gender, age and ethnicity, and had their weight and height measured. Weight and height measures were used to calculate BMI [(weight in kilograms)/(height in metres)²] and BMI categories were assigned according to WHO criteria (World Health Organization, 2000). BMI data were missing for one female participant in Caucasian data set A and one male participant in African data set B.

Each facial image was manually delineated by defining 179 feature points, and aligned according to interpupillary distance in PsychoMorph 8.4.7.0 (Benson & Perrett, 1993). This procedure standardises for head size.

3.2.1.3 Shape cue assessment

All data sets

Perimeter-to-area ratio was calculated for the lower half of the face for each image using in-house software. We specifically focused on the lower half of the face because the buccal fat pads are located in this region (Kahn, et al., 2000; Tostevin & Ellis, 1995). The perimeter was thus defined as the path along the horizontal line connecting the pupils and the perimeter of the face below the intersection with the interpupil line (Figure 5A). The area was defined as the area within this boundary (Figure 5A). The second measure, width-to-height ratio, was calculated as the horizontal distance between the two most lateral facial points (bizygomatic width or cheekbone width), divided by the vertical distance between the most inferior point of the upper eyelid and the most superior point of the upper lip (upper facial height; Figure 5B). This measure is similar to the width-to-height ratio defined by Carre' and McCormick (2008) and measures the relative width of the face. The third measure, cheek-to-jaw width, was calculated as the cheekbone width divided by the horizontal distance between the lateral points of the face along the midline of the lips (jaw width; Figure 5C). We were unable to identify the necessary landmarks for perimeter-to-area ratio measurements in 6 individuals (Caucasian A: 5 male; Caucasian B: 1 male) and cheek-to-jaw width ratio

measurements in 7 individuals (Caucasian A: 2 female; Caucasian B: 1 female, 3 male; African B: 1 male) because of facial hair covering the facial contours or slight lateral tilting of the face. These individual measures were therefore excluded from the study.

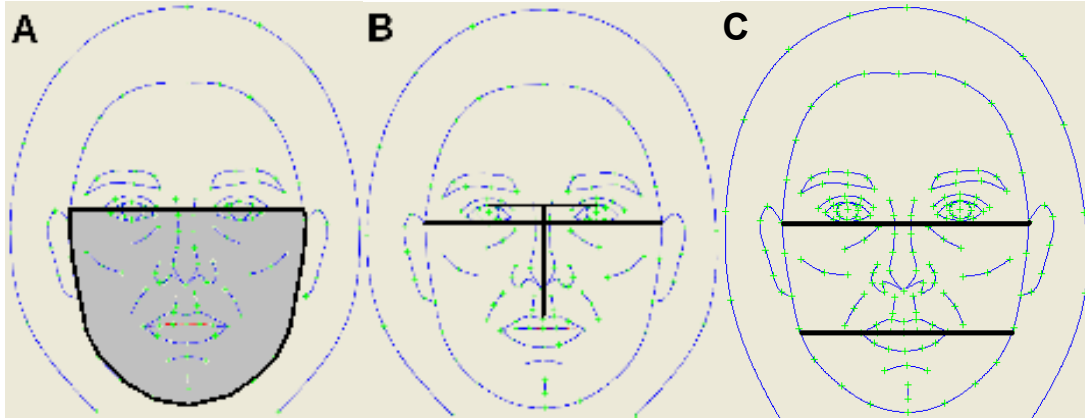


Figure 5. Measures used to calculate facial cues. (A) *Perimeter-to-area ratio: the perimeter is indicated in bold and the area as the shaded area within the perimeter.* (B) *Width-to-height ratio: cheekbone width divided by upper facial height (both indicated in bold).* (C) *Cheek-to-jaw width ratio: cheekbone width divided by jaw width.*

3.2.2. Results

3.2.2.1. Female faces

Each female data set was analysed separately. Skewness and kurtosis were low for all measures ($-0.7 < \text{skew}$ and $\text{kurtosis} > 1.1$), except for: the BMI measures of Caucasian data set B (skew 1.2, kurtosis 2.4) and African data set A (skew 1.6, kurtosis 2.1); the perimeter-to-area ratio measures of African data set A (kurtosis 2.3); the width-to-height measures of African data set A (kurtosis 2.3); and the cheek-to-jaw width measures of Caucasian data set A (kurtosis 1.3) and B (kurtosis 1.9). Conventional logarithmic and square root transformations could not successfully normalise the non-normal distributions, but reverse coding and power transformation (power 3) successfully normalised all the non-normal distributions ($-0.7 < \text{skew}$ and $\text{kurtosis} > 0.8$), except for the perimeter-to-area ratio and width-to-height measures of African data set A, so Spearman's correlations were used for this data set. Pearson's correlations were used for all other analyses. All correlations were two tailed. For ease of interpretation, we report the sign of the correlation coefficient, appropriate to original data, in cases where there

was reverse coding. We identified four influential outliers (leverage > 0.2). Throughout this study, results are reported both before and after the removal of outliers in cases where their removal influenced the statistical significance.

Width-to-height ratio correlated significantly with BMI in three of the four female data sets (Table 2). In the fourth data set, African A, width-to-height ratio correlated with BMI before ($r_{51} = 0.31$, $p = 0.028$), but not after the removal of one influential outlier, although a trend was evident (Table 2). The perimeter-to-area ratio did not correlate significantly with BMI in any of the data sets. The cheek-to-jaw width ratio correlated significantly with BMI in two of the four populations, while it tended to correlate with BMI in the third population (Table 2).

To test the overall association between these three measures (width-to-height ratio, perimeter-to-area ratio, cheek-to-jaw width ratio) and female BMI we performed fixed model meta-analyses in Comprehensive Meta-analysis v2.2.048 (Borenstein, Hedges, Higgins, & Rothstein, 2005). Data sets were weighted by their respective sample sizes. The meta-analyses indicated that overall both width-to-height ratio and the cheek-to-jaw width ratio correlated significantly with BMI, while the perimeter-to-area ratio did not (Table 2). The degree of multicollinearity between the three measures was fairly low (condition index < 2) with high tolerance values (width-to-height: 0.75; perimeter-to-area: 0.83; cheek-to-jaw: 0.67), indicating a high degree of independence between the three measures. Heavier women therefore had significantly wider (i.e. larger width-to-height ratio) and squarer (i.e. smaller cheek-to-jaw width ratio) faces than lighter women. The heavier women did not have significantly rounder lower faces (i.e. smaller perimeter-to-area ratio) as expected, but a trend was evident.

3.2.2.2. Male faces

Skewness and kurtosis were low for all measures ($-0.7 < \text{skew and kurtosis} > 1.1$), except for: the BMI measures of Caucasian data set A (skew 1.2, kurtosis 3.5) and African data set A (skew 1.3, kurtosis 2.1); and the width-to-height measures of African data set A (skew 1.8, kurtosis 5.7) and African data set B (kurtosis 3.0). Reverse coding and power transformation (power 3) successfully normalised all non-normal distributions

($-0.8 < \text{skew and kurtosis} > 0.8$). Pearson's correlations were used for all four data sets. All correlations were two tailed.

The results were less straightforward for the males than for the females. Width-to-height ratio correlated significantly with BMI in only one of the four male populations (Table 2). The perimeter-to-area ratio correlated significantly with BMI in two of the four populations (Table 2), while the cheek-to-jaw width ratio measure correlated significantly with BMI in only one population and showed a tendency to correlate with BMI in another (Table 2). Despite the lack of significance, width-to height ratio, perimeter-to-area ratio and cheek-to-jaw width ratio did show a consistent direction of relationships with BMI in all four populations (Table 2).

All three measures significantly correlated with male BMI in the meta-analyses (Table 2). Low multicollinearity (condition index < 2.2) and high tolerance values (width-to-height: 0.72; perimeter-to-area: 0.57; cheek-to-jaw: 0.75) indicated a high level of independence between the three measures. Heavier men therefore had significantly wider and squarer faces, with significantly rounder lower faces than lighter men.

Table 2: Correlations showing the relationship between BMI and the three quantifiable facial cues in four populations. The shaded section reports the results for the meta-analyses. Significant correlations are indicated in bold. All correlations are two tailed. $^{\delta} p \leq 0.1$; $* p \leq 0.05$; $** p \leq 0.01$; $*** p \leq 0.001$; $**** p \leq 0.0005$.

BMI	Female faces			Male faces		
	Width-to-height	Perimeter-to-area	Cheek-to-jaw	Width-to-height	Perimeter-to-area	Cheek-to-jaw
Caucasian A	0.48***	-0.10	-0.48**	0.33*	-0.38*	-0.31 ^{δ}
Caucasian B	0.39***	0.09	-0.11	0.12	-0.08	-0.11
African A	0.27 ^{δ}	-0.23	-0.33*	0.15	-0.31*	-0.10
African B	0.33*	-0.23	-0.25 ^{δ}	0.10	-0.16	-0.31*
Meta-analyses	0.36****	-0.12	-0.29****	0.17*	-0.22**	-0.20**

3.2.3. Discussion

The aim of this study was to find quantifiable cues to BMI, in 2D facial images. Perimeter-to-area ratio, width-to-height ratio and cheek-to-jaw width ratio relate to BMI in both Caucasian and African faces. In the females, width-to-height ratio and cheek-to-jaw ratio consistently, and significantly, relate to BMI, with heavier women having significantly wider and squarer faces than lighter women. Perimeter-to-area ratio did not significantly relate to female BMI in the meta-analyses, although it did show a consistent, albeit not significant, relationship with BMI in three of the four populations. It might therefore be slightly premature to exclude perimeter-to-area ratio as a weak cue to BMI in female faces. The relationship between these three quantifiable cues (width-to-height ratio, perimeter-to-area ratio and cheek-to-jaw ratio) and BMI was more irregular in the individual male populations than in the individual female populations, but overall all three measures were significantly related to BMI in the combined meta-analysis. Similar to the females, heavier men therefore also have significantly wider and squarer faces than lighter men. In addition, heavier men have significantly rounder lower faces than lighter men. Both the African and Caucasian populations showed similar associations between these measures and BMI, indicating that these might be cross-culturally invariant facial cues to BMI. In the next study we will test whether these cues relate to perceptual judgements of facial adiposity.

3.3. Study 2: The role of facial cues in the perception of facial adiposity.

3.3.1. Methods

3.3.1.1. Participants

Raters of Caucasian set A

26 Caucasian participants (14 female; mean age = 22.6, SD = 1.63, range = 21–24; 12 male, mean age = 23.0, SD = 3.04, range = 20–28) rated each female image for perceived facial adiposity on a seven-point Likert scale (0 = very underweight; 3 = average weight; 6 = very overweight). Another group of 29 Caucasian participants (17 female; mean age = 20.7, SD = 1.10, range = 19–23; 12 male; mean age = 20.8, SD =

2.29, range = 19–26) rated each male facial image for perceived facial adiposity on the same scale. Participants were shown all the images before rating commenced to make them aware of the range and variability of the images. Images were presented in a randomised order and participants were asked to indicate whether or not they knew the rated individual, if they did, rating data was excluded (5.8% of ratings). We recorded the time it took the participants to rate each image and excluded all participants with an average time of less than 1.65 seconds per question, for two or more images (3 females). The threshold value was defined by the maximum time it took the experimenter to select random answers as quickly as possible and included submission time. Full details on the ratings of Caucasian set A are available in (Coetzee, et al., 2009; chapter 2). Perceived facial adiposity ratings did not differ significantly between male and female raters for male ($p = 0.98$) and female images ($p = 0.48$). Data from both sexes were therefore combined in the analysis. Inter-rater reliability was very high (Cronbach $\alpha = 0.91$). Given the consistency of ratings, the scores were averaged across participants for each of the 84 images.

Raters of Caucasian data set B

Since we observed no significant difference in facial adiposity ratings between the sexes in the previous population, we recruited a new convenience sample of 35 participants (31 female; 4 male; mean age = 19.7, SD = 0.97, range = 18–22) from the University of St Andrews to rate the female images and the first 30 male images for facial adiposity. A further 35 participants were recruited (31 female; 4 male; mean age = 19.65, SD = 0.72, range = 18–22) from the University of St Andrews to rate the remaining 24 male images for facial adiposity. The methods were identical to the previous data set. We excluded 6 participants who fell below the threshold value for time. Inter-rater reliability was high (Cronbach $\alpha = 0.86$).

Raters of African data set A

We recruited another 33 participants (26 female; 7 male; mean age = 20.2, SD = 2.12, range = 18–27) from the University of St Andrews to rate the data set for facial adiposity. The methods were identical to those described for Caucasian data set A. We excluded 3 participants who fell below the threshold value for time. Inter-rater reliability was very high (Cronbach $\alpha = 0.94$).

All three studies were approved by the University of St Andrews ethics committee. African data set B was not rated for perceived facial adiposity.

3.3.2. Results

3.3.2.1. Female faces

Each female data set was analysed separately. Skewness and kurtosis were low for all perceived facial adiposity distributions ($-0.4 < \text{skew}$ and $\text{kurtosis} > 0.5$), the other measures were treated as in Study 1. We identified four influential outliers ($\text{leverage} > 0.2$). Throughout this study, results are reported both before and after the removal of outliers in cases where their removal influenced the statistical significance.

Width-to-height ratio correlated significantly with perceived facial adiposity in all three female populations (Table 2). Perimeter-to-area ratio also correlated significantly with perceived facial adiposity in all three populations (Table 2). The cheek-to-jaw width ratio correlated significantly with perceived facial adiposity in two of the three populations (Table 2).

To test the overall association between these three measures (width-to-height ratio, perimeter-to-area ratio and cheek-to-jaw width ratio) and perceived facial adiposity we performed fixed model meta-analyses in Comprehensive Meta-analysis v2.2.048. The meta-analyses indicated that overall all three measures correlated significantly with perceived facial adiposity (Table 2). Low multicollinearity (condition index < 2.0) and high tolerance values (width-to-height: 0.75; perimeter-to-area: 0.60; cheek-to-jaw: 0.82) indicated a high level of independence between the three measures. Women with relatively wider, squarer faces, and rounder lower faces, were perceived as being more overweight than women who did not have these characteristics.

3.3.2.2. Male faces

Skewness and kurtosis were low for all perceived facial adiposity measures ($-0.5 < \text{skew}$ and $\text{kurtosis} > 0.7$), the other measures were treated as in Study 1. We identified one influential outlier ($\text{leverage} = 0.42$).

Width-to-height ratio correlated significantly with perceived facial adiposity in two of the three male populations, while it tended to correlate with perceived facial adiposity in the third population (Table 2). The perimeter-to-area ratio correlated with perceived facial adiposity in all three populations (Table 2), while the cheek-to-jaw width ratio measure also correlated with perceived facial adiposity in all three populations (Table 2).

The meta-analyses indicated that overall all three measures correlated significantly with perceived facial adiposity (Table 2). Low multicollinearity (condition index < 2.3) and fairly high tolerance values (width-to-height: 0.67; perimeter-to-area: 0.57; cheek-to-jaw: 0.75) indicated a high level of independence between the three measures. Men with relatively wider, squarer faces, and rounder lower faces, were perceived to be more overweight than men without these characteristics.

Table 2: Correlations showing the relationship between perceived facial adiposity and the three quantifiable facial cues in three populations. The shaded section reports the results for the meta-analyses. Significant correlations are indicated in bold. All correlations are two tailed. ^δ $p \leq 0.1$; * $p \leq 0.05$; ** $p \leq 0.01$; * $p \leq 0.001$; **** $p \leq 0.0005$.**

Perceived facial adiposity	Female images			Male images		
	Width-to-height	Perimeter-to-area	Cheek-to-jaw	Width-to-height	Perimeter-to-area	Cheek-to-jaw
Caucasian A	0.50***	-0.34*	-0.61****	0.49***	-0.38*	-0.44**
Caucasian B	0.30*	-0.33*	-0.14	0.25 ^δ	-0.29*	-0.34*
African	0.50****	-0.43**	-0.70****	0.52****	-0.41**	-0.52****
Meta-analyses	0.43****	-0.37****	-0.51****	0.43****	-0.36****	-0.43****

3.3.3. Discussion

In this study we showed a strong association between the three quantifiable shape cues identified in Study 1 (width-to-height ratio, perimeter-to-area ratio and cheek-to-jaw width ratio) and perceived facial adiposity. People use these cues, or highly related

ones, to judge facial adiposity. In both males and females, individuals with wider, squarer faces and rounder lower faces are judged to be heavier than individuals with narrower, less square faces and less round lower faces. Interestingly, perimeter-to-area ratio is not significantly related to BMI in female faces, yet people still use it to judge facial adiposity. One plausible explanation for this is that people over-generalise by taking cues which are relevant elsewhere (i.e. in the body) and using them in the face.

3.4. General discussion

There were two main aims to this study. First, we wanted to identify quantifiable shape cues to BMI, in 2D facial images. Second, we wanted to determine if these cues are used in the perception of facial adiposity. We accomplished both aims.

In study 1, we identified three largely independent quantifiable cues that are closely related to BMI in African and Caucasian faces. Two of the cues, width-to-height ratio and cheek-to-jaw width ratio, were significantly related to BMI in both male and female faces. The third cue, perimeter-to-area ratio was significantly related to BMI in male, but not in female faces. We predicted that perimeter-to area ratio and cheek-to-jaw width ratio will decrease with increased BMI due to the increased buccal fat and masseter muscle volume. We also predicted that heavier individuals will have bigger frame sizes and therefore increased width-to-height ratios than lighter individuals. As a whole our results support these predictions, but future studies should test the associations between buccal fat volume, masseter muscle volume, frame size and BMI directly.

In study 2, we showed that people use these cues, or highly related ones, to judge facial adiposity. All three cues, width-to-height ratio, perimeter-to-area ratio and cheek-to-jaw width ratio, were very closely related to people's perception of facial adiposity in men and women, African and Caucasian. In fact, these cues were more closely related to perceived facial adiposity than to BMI. There are two plausible explanations for this. First, perceived facial adiposity might be based more on the percentage body fat while BMI is defined by body fat, muscle mass and frame size. If these cues are more closely related to body fat than to muscle mass and frame size, one would expect perceived facial adiposity to be more closely correlated with percentage body fat than BMI. Second,

individuals might be using these shape cues because they are more easily processable than other potential volumetric facial adiposity cues (shading for instance).

Our study focuses on facial cues to weight. In real life, body and facial information occur in conjunction, which may restrict generalization from the results presented here. Ratings of female images without clothing or with standardized clothing indicate that bodily and facial cues to attractiveness inter-correlate (Fink, et al., 2010; Hönekopp, et al., 2007; Peters, et al., 2007; Peters, Simmons, et al., 2008; Saxton, et al., 2009; Thornhill & Grammer, 1999; see discussion in section 1.3), but that the face and body cues provide independent contributions to overall attractiveness in both sexes (Peters, et al., 2007; Saxton, et al., 2009). Since the cues from the face and body contribute independently to overall attractiveness it is not unreasonable to study them separately. Of course, in normal situations cues from the body are obscured by clothing whereas for faces such confounds are reduced.

In summary, we identified three quantifiable facial cues that are both significantly related to BMI and are used to judge facial adiposity. Two of these cues, cheek-to-jaw width ratio and width-to-height ratio, were described as facial measures of sexual dimorphism by past research. BMI might therefore explain at least part of the interaction between sexual dimorphism and attractiveness observed in previous studies.

Chapters 4-6 restricted at the author's request
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Chapter 4

Is the most attractive facial adiposity also considered the healthiest?

This chapter is based largely on work that has been invited for resubmission in a peer-reviewed journal:

Coetzee, V., Perrett, D. I., Re, D., Tiddeman, B. P. & Xiao, D. Is the most attractive facial adiposity also considered the healthiest? *Body Image*.

Chapter 5

The media's portrayal of female body ideals in the United Kingdom, the United States and South Africa

This chapter is partly based on work that is currently under review in a peer-reviewed journal:

Coetzee, V., & Perrett, D. I. African and Caucasian body ideals in South Africa and the United States. *Eating Behaviors*.

Chapter 6

**Health and attractiveness preferences: an interplay
between cultural and environmental influences?**

7. Conclusions

In his classic 1979 book, *The Evolution of Human Sexuality*, Donald Symons presented evidence that human attractiveness evolved because of mate preference for healthy and fertile mates (Symons, 1979). The posited association between attractiveness and health is generally accepted, to the extent that Thornhill and Gangestad (1999a) referred to attractiveness as “a health certificate”. Yet, studies investigating the association between facial attractiveness and health have produced inconsistent results (see discussion in section 1.4). Furthermore, none of the well studied facial cues (e.g. symmetry, averageness and sexual dimorphism) have been reliably linked to both actual and perceived health (see discussion in section 1.6). Research on the relationship between skin condition and health does seem promising, but has only just taken off.

In the first chapter I discussed several plausible explanations for the discordance between studies investigating the relationship between facial attractiveness, the facial cues associated with attractiveness, and health, particularly indices of actual health. Some of the discordance between these studies could be explained by the way we measure health. For instance, although self-reported measures play a crucial role in psychology research because they are inexpensive and easy to obtain, studies could also benefit from including more direct health measures, such as blood pressure and hormonal analysis. Instead of just incorporating a range of different health measures, studies could benefit from taking a more directed approach, including health measures that are relevant to the facial cue in question. In addition, both perceived and actual health measures have their benefits and drawbacks, thus it is useful to include measures of both in studies testing the association between facial attractiveness, facial cues and health. Besides, in order for any facial cue to be a valid cue to health, the facial cue in question must be associated with both real health and the perception of health. Otherwise the facial cue is not really associated with health, or it is, but is of little value in mate choice.

Another plausible explanation for the discordance between facial cues and health is that variation in an unknown facial cue might disrupt the associations between well known facial cues (such as symmetry for example) and health. Using self-reported

(respiratory infections and antibiotics use), direct (blood pressure) and perceived measures of health I show that facial adiposity is reliably associated with both actual and perceived health, making it a valid cue to health. Not only is facial adiposity significantly associated with measures of both actual and perceived health, it also explains a substantial portion (~27%) of the variance in attractiveness judgments in both sexes. Future studies could investigate the inter-relationship between facial adiposity and other facial cues, such as symmetry, sexual dimorphism, averageness and skin condition, as it would be interesting to see how facial adiposity relates to these other facial cues. For instance, because carotenoids are stored in adipose tissue (El-Sohemy, et al., 2002), adipose tissue might serve as a 'sink' for carotenoids (e.g. the yellow and red skin pigments obtained from fruit and vegetables), producing a less yellow skin tone in overweight and obese individuals. Facial adiposity could also distort symmetry measurements, confounding the relationship between facial symmetry, health and attractiveness.

The way we measure facial cues could also explain some of the discordance between studies testing the relationship between facial cues and health. Both perceptual and quantitative measures of facial cues have their drawbacks, thus studies could benefit from using both perceptual and quantitative measures. In chapter 3, I identify three quantitative measures of facial adiposity that could in future be used to further test the association between facial adiposity and health.

Lastly, although the standard view on attractiveness is that attractiveness preferences are shared between cultures, recent work indicate that there is a variety of factors, such as environmental and conditional factors, that influence our views of attractiveness (see discussion in section 1.7.4). The studies reported here add to these recent findings, by showing that the association between health and attractiveness preferences for facial adiposity differs between cultures, and even within cultures. In chapter 4, and again in chapter 6, I show that Western Caucasian women prefer a significantly lower level of adiposity for attractiveness than for health in other women's faces. Contrary to Western women's preferences, Western Caucasian men and African observers show no significant difference between the levels of adiposity they consider 'most healthy' and 'most attractive'. I argue that the discrepancy between Western women's health and attractiveness preferences can most likely be explained by the

influence of the media, since the Western media portrays an exceptionally skinny ideal for female attractiveness (e.g. Spitzer, et al., 1999; Tovée, et al., 1997; chapter 5) and women are more likely to internalize this skinny ideal than men (Van den Berg, et al., 2007). Not only are men less likely to internalize media ideals, heterosexual men are also more constrained in their attractiveness preferences because health plays an important role in reproductive value (Symons, 1979), and therefore mate choice decisions. I also argue that the African observers in our study should show a closer association between health and attractiveness preferences than Western observers, which indeed they do, because these African observers live in an environment with a high disease burden, which would provide a selective pressure to base attractiveness preferences primarily on health. All, in all these studies indicate that a combination of environmental and cultural factors influence the association between attractiveness and health preferences cross-culturally.

There are some limitations to these studies that could be investigated in further work. For instance, we did not test the role of the media in facial adiposity preferences for health and attractiveness directly. It would also be helpful to compare health and attractiveness preferences across a wider range of cross-cultural populations. Lastly, in a study on bodies Tovée et al (2007) showed a relatively large discrepancy between health and attractiveness preferences for BMI amongst rural African observers in South Africa. These findings are inconsistent with our results showing a non-significant difference between the facial adiposity preferences for health and attractiveness in urban African observers in South Africa. There are various differences between the study reported in chapter 6 and that of Tovée et al (2007). Perhaps most importantly, I tested health and attractiveness preferences using faces from the observer's own ethnicity, while Tovée et al (2007) used images of Caucasian bodies to test African preferences. While my approach is ecologically more valid, Tovée et al's (2007) approach does have the advantage that both African and Caucasian observers were basing their preferences on a single set of images, whereas African and Caucasian participants in my study were basing their preferences on different sets of own-ethnicity images. One way of getting around this problem, and elucidating some of the differences between the two studies, is to perform a full cross-cultural study in which both African and Caucasian observers judge own-and-other ethnicity faces and bodies.

In summary, the work reported here identifies facial adiposity as a novel facial cue to health and attractiveness. Not only is facial adiposity a significant predictor of perceived health, but facial adiposity is also closely associated with indices of actual health in both sexes. Further work identified cross-cultural differences in the association between health and attractiveness preferences for adiposity, indicating that our concept of attractiveness is not culturally-invariant but differ depending on cultural and environmental influences.

8. References

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